Casuarina invasions: a multi-scale assessment of an important tree genus

by

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Thesis Outline

Understanding the processes that drive the invasion of non-native species is often essential for effective management. This thesis focuses on *Casuarina* spp. – an economically and ecologically important tree genus with taxa that have been widely disseminated by humans. I explore the effects certain taxa can have on community dynamics in recipient environments, investigate the factors that mediate invasion of *Casuarina* species, and from this aim to develop recommendations for managing the group.

First, I assessed the global introduction history, invasion ecology and the evolution of management approaches of *Casuarina*. Ten of the 14 species in the genus have been introduced outside their native ranges to over 150 countries, but only three species are recorded as naturalized or invasive. As with other groups there is a correlation between native range size and invasiveness – the three invasive species also have the largest introduced ranges. Propagule pressure explains much more of the variance in observed invasiveness between *Casuarina* taxa than any known combination of life-history traits. Large-scale plantings of casuarinas in some climatically suitable areas have not yet resulted in large-scale invasions; there is a substantial global *Casuarina* invasion debt. Experiences in Florida and the Mascarene Islands highlight that casuarinas have the potential to transform ecosystems with significant control costs. Despite modest progress with managing invasions in some areas, substantial problems remain. As with most other invasive tree taxa, complex conflicts of interest are particularly challenging.

Second, I looked at mechanisms underlying naturalization and assessed invasion risk at a regional scale. Here, I examined *Casuarina cunninghamiana* invasions in the south-western Cape of South Africa – the part of the country with the largest contiguous area climatically similar to the native range of the species. Propagule pressure is a key driver of naturalization of *C. cunninghamiana* populations in climatically suitable areas. The species also naturalizes in regions with suboptimal bioclimatic conditions, but then only very near (<10 m) planted trees. Risk models indicate that *C. cunninghamiana* is likely to spread across a greater region of the Western Cape than it currently occupies. Naturalized populations of *C. cunninghamiana* are young and expanding. The capacity of the species to resprout and attain reproductive maturity at an early age suggests that this species could become a widespread and damaging invader in South Africa. We conclude with some recommendations for

management, and argue that if particular steps are taken (e.g. the immediate removal of all female plants from proximity to dams and water-courses; all future sales and plantings to be restricted to male plants) then it might be possible to safely utilise the species in future.

Third, I examined the invasion dynamics of a single *Casuarina* species at the landscape scale. I explored how interactions between disturbance and invasion govern successional trajectories, using the remarkable invasion of *C. equisetifolia* on the volcanic island of Réunion. Invasive populations of *C. equisetifolia* have increased substantially in extent over 40 years. Lava flows have facilitated the spread of *C. equisetifolia* and invasion of this species has radically changed successional trajectories, increasing the rate of succession sevenfold. This case mirrors work done on *Morella faya* and *Falcataria moluccana* on Hawa'ii, which shows the extent to which invasive species can alter ecosystem function and benefit from natural disturbances generated by volcanic lava flows. The continued spread of *C. equisetifolia* poses a major threat to the small area of remaining native lowland rainforests on Réunion which cover < 2 % of their original extent.

The studies in this thesis have uncovered patterns, processes and invasion risks for invasive trees that are not well represented in the literature. Some insights derived from well-studied tree genera, such as *Acacia* and *Pinus*, seem to apply fairly well to tree invasions in general. However, special ecological features of *Casuarina* species and the ways they are used by humans call for unique considerations when piecing together changing global distributions and creating effective strategies for management.

Opsomming

‘n Deeglike begrip van die prosesse wat die indringing van uitheemse spesies fasiliteer is noodsaaklik vir effektiewe besturing. Hierdie tesis fokus op *Casuarine* spp. – ‘n ekonomiese en ekologiese belangrike boom genus, met menigte spesies binne hierdie genus wyd verspreid deur mense. Ek ondersoek die effekte wat sekere taksa kan hê op die gemeenskap dinamika in die ontvanger omgewing, sowel as die faktore wat *Casuarina* indringing bemiddel, en deur hierdie doelwitte beoog ek om aanbevelings te maak aangaande die effektiewe bestuur van hierdie groep.

Eerstens evalueer ek die invoerings geskiedenis van die genus wêreldwyd, die indringer ekologie en ook die evolusie van bestuurs benaderinge ten opsigte van *Casuarina*. Tien van die 14 spesies binne hierdie genus is ingevoer na meer as 150 verkillende lande buite hul inheemse streek, maar slegs drie van hierdie spesies word beskou as genaturaliseerd of indringers. Soos met ander groepe is daar ‘n korrelasie tussen inheemse streeks-grote en indringerheid – die drie indringer spesie het ook die grootste ingevoerde streke. Propaguul druk verduidelik die meerderheid van die variasie in die waargeneme indringer *Casuarina* taksa as enige ander kombinasie van lewens geskiendenis eienskappe. Groot skaalse plantasies van casaurina taksa in sommige klimaat geskikste areas het nog nie na groot skaalse indringing gelei nie; daar is wêreldwyd ‘n aansienlike *Casuarina* indringer skuld. Ervarings in Florida en die Mascarene Eilande beklemtoon dat casuarinas die potensiaal het om ekosisteme te transformeer met geweldige beheer omkostes. Ten spyte van redelike vordering aangaande die besturing van indringers in sekere areas, is daar steeds aansienlike probleme. Soos met meeste ander indringer boom taksa, is die botsing van belange veral uitdagend.

Tweedens, het ek die meganismes van die naturalisasie bemiddel as ook indrigner risiko op die plaaslike skaal ondersoek. In hierdie deel het ek *Casuarina cunninghamiana* indringers in die Suid-Wes Kaap van Suid-Afrika ondersoek – die deel van die land met die grootste aangrensende area wat ‘n ooreenstemmend klimaat het met die inheemse areas van die spesie. Propaguul druk is ‘n belangrike drywer vir die naturalisasie van *C. cunninghamiana* populasies in areas met ‘n geskikte klimaat. Hierdie spesie het ook genaturaliseer in areas met suboptimale klimaats kondisies, maar slegs baie naby (<10m) aan plantasies. Risiko modelle dui aan dat *C. cunninghamiana* die potensiaal het om te versprei na ander dele van die Wes-

Kaap waar dit huidiglik afwesig is. Natuurlike populasies van *C. cunninghamiana* is jonk en in die proses van uitbreiding. Die kapasiteit van die spesie om te hergrooi en voortplantings volwassenheid op n vroeë ouderdom te beriek stel voor dat hierdie spesie ‘n wyd verspreide en skadelike indringer kan word. Ons sluit af met aanbevelings vir effektiewe bestuur en stel voor dat indien sekere stappe geneem word (bv. ontmiddelike verwydering van die vroulike plante naby damme en water areas; alle verdere verkope beperk word tot manklike plante), dit moontlik sal wees om hierdie spesie op ‘n omgewings-veilige manier te gebruik.

Derdens het ek die indringing dinamika van ‘n enkele *Casuarina* spesie on landskap skaal ondersoek. Ek het verken hoe interaksies tussen versteurings en indringing plantegroei prosesse dryf, deur gebruik te maak van die merkwaardige indringing van *C. equisetifolia* op die vulkaniese eiland van Reunion. Indringer populasies van *C. equisetifolia* het aansienlik vermeerder in die afgelope 40 jaar. Lava vloei het die verspreiding van *C. equisetifolia* gefasiliteer en indringing van hierdie spesie het plantegroei prosesse radikaal verander, deur die tempo van opvolging sewevoudig te verhoog. Hierdie studie weerspieël werk wat op *Morella faya* en *Falcataria moluccana* in Hawa’ii gedoen is en toon tot watter mate indringer spesies ekosisteem funksies kan verander en voordeel kan trek uit natuurlike versteurings wat gegenereer word deur vulkansiese lava vloei. Die voortgesette verspreiding van *C. equisetifolia* hou ‘n groot bedreiging in vir oorblywende inheemse laeveld reënwoude op Reunion wat tans < 2% van hul oorspronlike area dek.

Die studies in hierdie tesis het patrone, prosesse en indringer risikos vir indringer bome ontdek wat nie goed in die literatuur verteenwoodig word nie. Sommige insigte wat deur goed bestudeerde boom genera, soos *Acacia* en *Pinus,* ontdek is, blyk om redelik goed van toepassing te wees op boom indringers in geheel. Alhoewel, sekere ekologiese funksies van *Casuarina* spesies en die manier wat hulle deur mense gebruik word, vra vir unieke oorwegings aangaande hul wêreldwye verspreiding en effektiewe beheer.

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For further details see the acknowledgements section in chapter three and four.

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Chapter 1: Introduction

Biological invasions are a major threat to biodiversity and ecosystem functioning worldwide (Mack et al., 2000); this is largely attributed to the increase in global trade (Vitousek et al., 1997). Until recently, trees were not widely considered as important invasive species (Richardson and Rejmánek, 2011), but following the human-mediated movement of thousands of tree species around the world for many purposes in the past few centuries, the phenomenon of widespread alien tree invasions has increased in importance (Richardson et al., 2008).

Each stage of the introduction-naturalization-invasion continuum (sensu Richardson et al., 2000) is influenced by ecological processes that operate at different spatial scales (Pauchard and Shea, 2006). The effects of invasions are also multi-scalar and can affect community structure, ecosystem processes and functioning, and the nature and intensity of ecological interactions (Brown et al., 2008). It has become increasingly apparent that multi-scale analyses of invasions are needed to identify and elucidate the mechanisms driving biological invasions, and to define effective management strategies (Mack, 2000; Pauchard and Shea, 2006).

1.1 Global natural experiment

Tree species have been introduced into different environments, at different times, for different purposes where various human activities and environmental disturbances have facilitated establishment (Richardson and Rejmánek, 2011; Richardson et al., 2011). Many invasive tree species have notable benefits to humans besides the undesirable impacts that occur in parts of their introduced ranges (McNeely, 2001). Conflicts of interest often arise when the benefits species provide are weighed against the costs (De Wit et al., 2001; Richardson and van Wilgen, 2004). Species that cause such conflicts of interest pose special challenges for those tasked with managing natural resources (Richardson et al., 2011).

A better understanding of the determinants of naturalization is important as all naturalized species are potential invaders. A strong link exists between suites of traits and invasiveness (Richardson and Pyšek, 2012). Species traits such as fast growth, high seed production and resprouting ability often promote invasiveness in woody plants. However, successful invasions also depend on the characteristics of the receiving environment (Alpert et al., 2000;

Richardson and Pyšek, 2006). Identifying areas at risk to invasions and predicting spread pathways of invasive species can improve the efficiency of search and management strategies (Rouget et al., 2002; Trethowan et al., 2011).

1.2 Consequences of tree invasion

Biological invasions can lead to drastic changes in ecosystem functioning (Lamarque et al., 2011). These effects are particularly prominent on oceanic islands where many ecosystems have been disrupted by invasive species (Vitousek and Walker, 1989; Kueffer et al., 2010). Biological invasions on oceanic islands provide a useful system for examining the effects of individual species on ecosystem-level phenomena (Vitousek & Walker 1989; Kueffer et al., 2010). Current impacts by plant invaders highlight the importance of identifying which species have the potential to successfully invade once introduced into a novel range. For example, work on *Falcataria moluccana* and *Morella faya* on Hawa'ii has shown the extent to which invasive species can alter ecosystem function and benefit from natural disturbances generated by volcanic lava flows (Vitousek and Walker 1989, Lenz and Taylor 2001; Hughes and Denslow, 2005). Because of their long history of large-scale disturbances (natural and anthropogenic) and introduction of non-native species, oceanic islands can serve as early warning systems for continental systems that have yet to experience such a disturbance history (Kueffer et al., 2010).

1.3 *Casuarina*

Important model groups of woody plants such as Australian *Acacia* species (Castro-Díez et al. 2011; Hui et al. 2011; Kull et al. 2011; Richardson et al., 2011) and *Pinus* (Richardson, 2006) have been well studied in the field of plant invasion biology. Like these model groups, many *Casuarina* species have a long history of introduction to regions outside their native ranges for various economic, ecological and social purposes. Certain life-history traits such as symbiotic N-fixing associations with soil actinomycetes and mycorrhizal fungi, rapid growth rates and prolific seed production predispose some casuarinas to become naturalized in their new ranges. Unlike the aforementioned genera, casuarinas have rarely been planted for commercial purposes and therefore exhibit different introduction patterns. Consequently, different types of ecosystems are exposed to invasions - making this group functionally unique. The long history of widespread transfers and planting of *Casuarina* species in many parts of the world has created a global-scale natural experiment with many opportunities to explore different aspects of plant invasion ecology (Richardson, 2006).

Given these features, *Casuarina* represents an excellent study group for uncovering patterns, processes and invasion risks that are not well represented in better studied model groups.

1.4 Aim and objectives

The overall aims of the studies in this thesis were to investigate the importance of *Casuarina* as a model genus, investigate factors mediating invasion, provide recommendations for management, and explore the effects certain taxa can have on community dynamics in their recipient environments.

This was accomplished by: 1) identifying drivers of introduction and invasion of *Casuarina* species on a global scale (Chapter 2); 2) examining the mechanisms underlying naturalization, assessing invasion risk on a regional scale, and providing recommendations for control (Chapter 3); 3) assessing the invasion dynamics of a single *Casuarina* invasion at a landscape scale (Chapter 4).

1.5 Chapter Synopsis

This thesis comprises three research chapters which are presented in the form of manuscripts to be submitted to scientific journals. A multi-scale approach was taken to provide useful insights on the rationale behind human-mediated introductions, the effects that invasive species have on community dynamics, the determinants of invasion, and potential management approaches in different parts of the world for a globally important group of plants.

First, I mapped current global distributions, and modelled the potential global distribution of the *Casuarina* genus. I assessed the history of introductions, the status of introduced species on the introduction-naturalization-invasion continuum, correlates of invasive success, impacts of invasions, and the evolution of management approaches. This global perspective also provided the means for predicting likely outcomes of introduction in different parts of the world, since many plantings have been recent (Chapter 2).

Second, I collated information on the distribution of planted versus naturalized individuals of *C. cunninghamiana* in one part of its South African range: the south-western part of the Western Cape. I examined differences between naturalized and non-naturalized populations (sensu Pyšek et al., 2004). This information was used to identify correlates of naturalization

and invasion and to identify areas at risk of invasion by *C. cunninghamiana*, and provide recommendations for control (Chapter 3).

Third, I explore how interactions between disturbance and invasion govern successional trajectories, using the remarkable invasion of *C. equisetifolia* on the volcanic island of Réunion as a case study. I collated all available records on the distribution of *C. equisetifolia* from surveys undertaken in 1972 and 1990, and collected spatially-explicit information on tree height, abundance and density during detailed field surveys conducted in 2012. I compared all results from the three surveys to assess how the invasion has progressed over 40 years by exploring the roles of distance to source, altitude, and lava flow age. I also present a conceptual model comparing natural and invaded successional processes in light of natural and human-mediated disturbances (Chapter 4).

Finally, I provide a synthesis of what the results of the work presented in the three research chapters add to our knowledge of plant invasion ecology (Chapter 5).

References

Alpert, P., Bone, E., Holzapfel, C., 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3, 52–66.

Brown, K.A., Spector, S., Wu, W., 2008. Multi-scale analysis of species introductions: combining landscape and demographic models to improve management decisions about non-native species. Journal of Applied Ecology 45, 1639–1648.

Castro-Díez, P., Godoy, O., Saldaña, A., Richardson, D.M., 2011. Predicting invasiveness of Australian acacias on the basis of their native climatic affinities, life history traits and human use. Diversity and Distributions 17, 934–945.

De Wit, M.P., Crookes, D.J., van Wilgen, B.W., 2001. Conflicts of interest in environmental management: estimating the costs and benefits of a tree invasion. Biological Invasions 3, 167–178.

Hughes, F., Denslow, J.S., 2005. Invasion by a N_2-fixing tree alters function and structure in wet lowland forests of Hawai'i. Ecological Applications 15, 1615–1628.

Hui, C., Richardson, D.M., Robertson, M.P., Wilson, J.R.U., Yates, C.J., 2011. Macroecology meets invasion ecology: linking native distribution of Australian acacias to invasiveness. Diversity and Distributions 17, 872-883.

Kueffer, C., Daehler, C.C., Torres-Santana, C.W., Lavergne, C., Meyer, J-Y., Otto, R., Silva, L., 2010. A global comparison of plant invasions on oceanic islands. Perspectives in Plant Ecology, Evolution and Systematics 12, 145–161.

Kull, C.A., Shackleton, C.M., Cunningham, P.S., Ducatillon, C., Dufour-Dror, J.-M., Esler, K.J., Friday, J.B., Gouveia, A.C., Griffin, A.R., Marchante, E.M., Midgley, S.J., Pauchard, A., Rangan, H., Richardson, D.M., Rinaudo, T., Tassin, J., Urgenson, L.S., von Maltitz, G.P., Zenni, R.D., Zylstra, M.J., 2011. Adoption, use, and perception of Australian acacias around the world. Diversity and Distributions 17, 822-836.

Lamarque, L.J., Delzon, S., Lortie, C.J., 2011. Tree invasions: a comparative test of the dominant hypotheses and functional traits. Biological Invasions 13, 1969-1989.

Lenz, L., Taylor, J.A., 2001. The influence of an invasive tree species (*Myrica faya*) on the abundance of a non-native insect (*Sophonia rufofascia*) in Hawai'i Volcanoes National Park. Biological Conservation 102, 301–307.

Mack, R.N., 2000. Assessing the extent, status and dynamism of plant invasions: current and emerging approaches. In: Mooney, H.A., Hobbs, R.J. (Eds.), Invasive Species in a Changing World. Island Press, Washington, D.C. pp 141–168.

Mack, R.N., Simberloff, D., Lonsdale, M., Evans, H., Clout, M., Bazzaz, F., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10, 689–710.

McNeely, J.A., (Ed) 2001. The great reshuffling: the human dimension of invasive alien species. IUCN, Gland, Switzerland.

Pauchard, A., Shea, K., 2006. Integrating the study of non-native plant invasions across spatial scales. Biological Invasions 8, 399–413.

Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G., Williamson, M., Kirschner, J., 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53, 131–143.

Richardson, D., Pyšek, P., 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography 30, 409-431.

Richardson, D.M., 2006. *Pinus*: a model group for unlocking the secrets of alien plant invasions? Preslia 78, 375–388.

Richardson, D.M., Carruthers, J., Hui, C., Impson, F.A.C., Miller, J.T., Robertson, M.P., Rouget, M., Le Roux, J.J., Wilson, J.R.U., 2011. Human-mediated introductions of Australian acacias – a global experiment in biogeography. Diversity and Distributions 17, 771–787.

Richardson, D.M., Pyšek, P., 2012. Naturalization of introduced plants: Ecological drivers of biogeographic patterns. New Phytologist 196, 383–396.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, D.F., West, C.J., 2000. Naturalization and invasion of alien plants - concepts and definitions. Diversity and Distributions 6, 93-107.

Richardson, D.M., Rejmánek, M., 2011. Trees and shrubs as invasive alien species – a global review. Diversity and Distributions 17, 788–809.

Richardson, D.M., van Wilgen, B.W., 2004. Invasive alien plants in South Africa: how well do we understand the ecological impacts? South African Journal of Science 100, 45–52.

Richardson, D.M., van Wilgen, B.W., Nuñez, M., 2008. Alien conifer invasions in South America – short fuse burning? Biological Invasions 10, 573–577.

Rouget, M., Richardson, D.M., Nel, J.A., van Wilgen, B.W., 2002. Commercially-important trees as invasive aliens - towards spatially explicit risk assessment at a national scale. Biological Invasions 4, 397-412.

Trethowan, P.D, Robertson, M.P., McConnachie, A.J., 2011. Ecological niche modelling of an invasive alien plant and its potential biological control agents. South African Journal of Botany 77, 137-146.

Vitousek, P.M., Dantonio, C.M., Loope, L.L., Rejmanek, M., Westbrooks, R., 1997. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21, 1–16.

Vitousek, P.M., Walker, L.R., 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. Ecological Monographs 59, 247–265.

Chapter 2: *Casuarina*: biogeography and ecology of an important tree genus in a changing world

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DMR: Provided comments on the manuscript and improved the writing, and sourced species information for the database from international experts.
JRUW: Provided comments on the manuscript and statistical advice.

Intended journal: *Biological Invasions*

2.1 Abstract

Important insights on the invasion ecology of woody plants are emerging from the study of model groups, but it is important to test whether such results can be generalised. We examined whether drivers of introduction and invasion in the genus *Casuarina* are similar to those identified for other groups. We reviewed the literature, mapped current global distributions, and modelled the potential global distribution of the genus. We assessed the rationale behind introductions, impacts of invasions, and the evolution of management approaches. Casuarinas have been introduced to about 150 countries. Ten of the 14 species in the genus have been introduced outside their native ranges, but only three species are recorded as naturalized or invasive (*C. equisetifolia*, *C. cunninghamiana* and *C. glauca*). Species with a large native ranges are more likely to be introduced and invasive; the three invasive species also have the largest introduced ranges. There were no clear relationships between life-history traits (e.g. seed mass, plant height, or resprouting ability) and the extent of invasion. About 8 % of the Earth's land surface is potentially suitable for casuarinas and large-scale plantings in some climatically suitable areas have not yet resulted in large-scale invasions; there is a substantial global *Casuarina* invasion debt. Experiences in Florida and the Mascarene Islands highlight that casuarinas have the potential to transform ecosystems with significant control costs. The challenge is to develop management approaches that minimise the impacts of invasions while preserving economic, environmental and cultural values of species in their introduced ranges.

Keywords Biological invasions, *Casuarina*, ecology, introduction, native range, management, tree invasions.

2.2 Introduction

Species from all taxonomic groups are being moved around the world accidentally and intentionally by humans at unprecedented rates (Ricciardi 2006; Wilson et al. 2009). Many of these organisms have notable benefits to humans, but some have undesirable consequences in parts of their introduced ranges (McNeely 2001). As human populations grow and concerns regarding the sustainability of different forms of land use increase, more attention is being given to evaluating both the costs and benefits of introduced species. Some introduced species spread from sites of introduction to invade ecosystems where their presence may alter the structure and functioning of such ecosystems. In some cases, such invasive species bring about changes that are deemed undesirable and which may cause widespread degradation of ecosystems resulting in substantial costs (Pyšek and Richardson 2010).

Important insights have emerged in recent decades on many aspects of the numerous processes that determine which organisms are moved by humans and how they are moved and disseminated, the features of species and environments that facilitate establishment, proliferation and spread, and the many facets that need to be considered when attempting to manage introduced species (Richardson 2011). Much work has focussed on trying to understand the full range of processes involved in the movement of woody plant species around the world (Richardson and Rejmánek 2004; 2011), their performance as alien species (Rejmánek and Richardson 1996), and on developing effective management methods (e.g. Richardson 1998; Wilson et al. 2011). Trees did not, however, feature prominently on lists of the most problematic invasive species until recently (Richardson and Rejmánek 2011). But, following the widespread transport and use of thousands of tree species for many purposes in all parts of the world in the past few centuries, the phenomenon of widespread invasions of alien trees is rapidly increasing in importance (Richardson et al. 2008; Richardson and Rejmánek 2011). Comparisons between the performances of species in different situations around the world is important for developing protocols for screening new introductions for invasiveness and for managing species that may become or have already become invasive (Richardson et al. 2008; Simberloff et al. 2010).

Global syntheses of the invasion ecology of particular genera or groups (Richardson and Bond 1991; Richardson and Rejmánek 2004; Williamson and Smith 2007; Dogra et al. 2010; Richardson et al. 2011) have considerable value because: invasiveness in one part of the world is possibly the best predictor of likely invasiveness in climatically similar regions

(Richardson and Rejmánek 2004; Hulme 2012); each planting in a new locality represents a test of the determinants of invasiveness and invasibility (Richardson et al. 1994; 2011); and management lessons in one area can be transferred to other regions (e.g. Richardson et al. 2008; Wilson et al. 2011). It is important to consider whether such comparisons yield broad generalities or whether generalisations apply only to a subset of model taxa.

The genus *Casuarina* represents an interesting case study. Like other genera of trees that have been widely planted outside their native ranges (notably *Acacia*, *Eucalyptus* and *Pinus*; Richardson 1998), the global distribution of the genus *Casuarina* has been radically changed by humans in the last few centuries. Unlike the aforementioned genera, no attempt has been made to assess the stage of the global transplant experiment for *Casuarina*, nor the status of each species in terms of naturalization and invasion. The distinct evolutionary lineage of Casuarinaceae (a Gondwanan family with a unique combination of morphological characters; Steane et al. 2003), its widespread distribution, and the economic and ecological significance of its species, makes it an important lineage to compare to existing model taxa. Research on this genus may therefore help to uncover patterns, processes and invasion risks that are not well represented in better studied model groups. Using *Casuarina* species as a model group, we explore the following questions: How far advanced is the natural experiment of global introductions compared to that for other model groups? Do features of the native range tell us anything about potential invasiveness? Does the link between planting intensity and degree of invasion in casuarinas differ from that of Australian acacias, eucalypts and pines? Does a large introduced range coupled with key life-history traits predispose some casuarinas to become naturalized in their new ranges? Are casuarinas likely to become more widespread invaders and appear on lists of invasive species in many more areas in the future?

2.3 Casuarinas at home

Species in the genus *Casuarina*, commonly known as casuarinas, beefwoods, she-oaks, Australian pines or ironwoods, are fast-growing evergreen trees native to Australia, Southeast Asia and the Pacific archipelagos (Wheeler et al. 2011). The family Casuarinaceae includes 4 genera and about 96 species (Wilson 1997; Steane et al. 2003). The number of species in the genus *Casuarina* has been widely debated in the literature. Torrey and Berg (1988) recognized 16 species in the genus, but more recent studies have accepted 17 valid species (Steane et al. 2003; Chezhian et al. 2009; Gaskin et al. 2009; Taylor et al. 2010; Ogunwande et al. 2011; Wheeler et al. 2011), while Boland et al.'s (1996) treatment, in agreement with

those of Zhongze and Torrey (1985) and Savourie and Lim (1991), recognize 15 taxa: 11 full species, four of which have two subspecies each. In this paper we use the treatment presented in The Plant List (2010) - currently the most comprehensive authoritative list for plant names (Kalwij 2012). The 19 taxa, including 14 species, are listed in Table 2.1.

Casuarina equisetifolia has the largest native range of the species in the genus (Parrotta 1993), and occurs in coastal regions of Northern Australia, Malaysia and Southeast Asia, and Oceania (Parrotta 1993; Rogers and Gamble 2008, Swearingen 1997). It is mostly confined to a narrow strip adjacent to sandy coasts, rarely extending inland. *Casuarina cunninghamiana* has an extensive native range in temperate and subtropical areas along the eastern and northern coasts of Australia. Its ability to withstand periodic inundation makes it important for protecting river banks from erosion (U.S. National Research Council 1984). The native range of *C. glauca* is narrower, extending along the eastern coast of Australia from New South Wales to Queensland (Blombery 1977; Boland et al. 1984). *Casuarina cristata*, native to eastern Australia, occurs in woodlands and open forests. It is a valued source of shade, shelter, timber, and as emergency drought fodder (U.S. National Research Council 1984). *Casuarina obesa* is common in southern Western Australia, but also occurs in central South Australia, north western Victoria and south western New South Wales (Emmott 2001). In southern Western Australia, it has been used extensively to revegetate saline and waterlogged areas. *Casuarina pauper* (closely related to *C. cristata*) is native to southern Australia where it is usually found growing with Slender Cypress-pine (*Callitris gracilis*) in open woodlands on sandy rises (Victorian Resources Online 2011). It produces a very dense wood suitable for fencing, fuel and wood-turning. *Casuarina junghuhniana* is native to Indonesia where it grows naturally on the slopes of volcanoes and is a pioneer species of deforested land (Orwa et al. 2009). It is drought-tolerant and can survive prolonged waterlogging due to its ability to tolerate oxygen deficiency (Orwa et al. 2009). *Casuarina grandis*, native to Papua New Guinea, forms dense stands along rivers and regenerates on gravel banks and open sites (U.S. National Research Council 1984). *Casuarina oligodon*, native to Indonesia and Papua New Guinea (Bourke 1985), occurs at high elevations where it forms extensive pure stands along river beds and on ridge tops (U.S. National Research Council 1984). It is widely used as a windbreak in its natural range where it is often planted around villages to provide protection against strong winds (Orwa et al. 2009). It is a popular subsistence crop for food gardens as well as a fallow intercrop (Vergara and Nair 1985). *Casuarina orophila*, also native to Papua New Guinea, is not mentioned in the literature. *Casuarina collina* is native to New Caledonia

(Gauthier et al. 1999). Natural stands often occur in riparian ecosystems, but the species is abundant on a wide range of soils (Gauthier et al. 1999). This fire-resistant species can quickly colonise disturbed areas (Gauthier et al. 1999). For these reasons, *C. collina* has a high potential for rehabilitation of degraded lands in New Caledonia where nickel mining generates large areas of sterile and toxic lands (Gauthier et al. 1999). Other *Casuarina* species native to New Caledonia not mentioned in the literature include *C. potamophila, C. tenella and C. teres.*

The phylogenetic and biogeographic relationships of the genus are complex. A phylogenetic study of Casuarinaceae placed all species native to Australia (*C. cristata*, *C. cunninghamiana, C. glauca, C. obesa and C. pauper*) in the same clade, while the species with native ranges extending further north (Indo-malesia, New Caledonia and Papua New Guinea) were grouped into the same clade (Steane et al. 2003). Although the native range of *C. equisetifolia* (a coastal species) remains uncertain (Elevitch 2006), natural dispersal methods (e.g. sea-drift may explain its wide distribution. The grouping of *C. equisetifolia* with Indo-malesian species (*C. collina*), rather than the endemic Australian species, suggests that *C. equisetifolia* is either a relatively new species that established in Australia from Indo-malesia, or one that evolved in Australia from a shared ancestor with other Indo-malesian taxa and then dispersed to other regions (Steane et al. 2003). *Casuarina oligodon* forms a separate clade.

Casuarina species are valued and protected trees in their native range for evolutionary, biodiversity and cultural reasons (Boland et al. 1984). The bark of some species is used by Australian aborigines to construct canoes (Flannery 1999). Some vegetation types dominated by *Casuarina* are of high priority for conservation, e.g. the threatened Belah and Coolibah woodland habitat comprising *C. cristata*, *Eucalyptus coolabah* and *Muehlenbeckia cunninghamii*. Casuarinas also form important habitat for rare animals. For example, the vulnerable Glossy black cockatoo (*Calyptorhynchus lathami*) and the Red-winged parrot (*Aprosmictus erythropterus*) inhabit eucalypt and *C. cunninghamiana* woodlands of which only 25% remains (Joseph 1982; Chapman 2007). *Casuarina cunninghamiana* woodlands are also an important habitat for the critically endangered Regent Honeyeater (*Anthochaera phrygia*) (Menkhorst et al. 1999). Casuarinas also provide important habitat for the vulnerable Black Grass Dart butterfly, *Ocybadistes knightorum* Lambkin and Donaldson (Lepidoptera: Hesperiidae; Sands and New 2002) and are hosts for various epiphytic orchids

(Blombery 1977). Although widespread in southern Western Australia, *C. obesa* has listed as threatened in Victoria under the Flora and Fauna Guarantee Act 1988 (Blake 2009).

2.4 The current global distribution of casuarinas

Because of the economic importance of many *Casuarina* species (Fig. 2.1), they have been introduced to areas around the world where some species have become naturalized or invasive (Fig. 2.2). The Australian Tree Seed Centre (ATSC) played a major role in the collection, storage and dissemination of *Casuarina* seeds from the 1980s onwards (Midgley 1990). During the 1980s, seedlots of casuarinas were dispatched to a total of 103 countries. The main recipients were Asia (35% of all seed-lots); Australia (23%); Africa (19%); Central and South America (8%); North America (5%); South Pacific (3%); Middle East (2%) and Indian Ocean Islands (1%). Most of this seed was distributed to Australia, Bangladesh, Brazil, China, Egypt, India, Kenya, Pakistan, Philippines, Thailand and USA (Midgley 1990). ATSC focussed on seven species: *C. cunninghamiana* - to 85 countries; *C. equisetifolia* – 68; *C. glauca* – 66; *C. cristata* – 51; *C. obesa* – 43; *C. junghuhniana* – 17; and *C. oligodon* – 15 (Midgley 1990). The percentage of *Casuarina* seed dispatched from the ATSC is likely to have decreased from this time due to an increased demand for other genera and a growing preference for a few *Casuarina* species, notably *C. cunninghamiana*, *C. equisetifolia*, *C. glauca* and *C. obesa*. In the past, the ATSC has been unable to meet the demand for high priority, non-Australian species such as *C. junghuhniana*, *C. grandis* and *C. oligodon* (Midgley 1990). Table S2.1 shows dates of introduction and large-scale cultivation for all *Casuarina* species around the world.

The species richness of *Casuarina* around the world was mapped at a resolution of 15 x 15 decimal degrees following the methodology of Procheş (2006) and Procheş et al. (2012) using ESRI ArcView v.10.0 (Fig. 2.3). Occurrence records for each species from several databases, namely the Invasive Species Compendium (CAB International 2000, http://www.cabi.org/ISC/), Global Biodiversity Information Facility (GBIF 2008, http://www.gbif.org) and Atlas of Living Australia (www.ala.org.au/), were used to map the native, introduced and naturalized ranges of each species. The resolution of current climate data is inadequate for accurately modelling species distributions on islands given their rugged topography and/or complex microclimates.

Casuarinas are now found across most tropical and sub-tropical regions, with many species in China, India, Kenya, Senegal and Tanzania (Fig. 2.3b). Despite the paucity of published sources for most parts of Africa, various unpublished sources and anecdotal evidence indicates that the genus has been widely disseminated throughout the continent. Introductions have resulted in the naturalization and invasion (sensu Pyšek et al. 2004) of three species in many parts of the world (Fig. 2.3c).

2.5 The potential global distribution of casuarinas

A close match between broad-scale climate in the native and receiving ranges is an important requirement for naturalization and invasion of alien plants (Richardson and Pyšek 2012). Species with large climatic or geographical native ranges are more likely to become invasive elsewhere (van Kleunen et al. 2011). To derive a rough estimate of climatic suitability and therefore the potential global range of casuarinas, we built bioclimatic models for each species using MaxEnt v3.3.3 (Phillips et al. 2006; Fig. 2.3d; Figure S2.2). We compiled occurrence records from Australia's Virtual Herbarium (avh.ala.org.au/). Nine interpolated bioclimatic variables (2.5 min spatial resolution) were obtained from WorldClim (http://www.worldclim.org, Hijmans et al. 2005) and used as predictor variables for developing simple climate envelope models for each species. The climatic variables used were: annual mean temperature, isothermality, temperature seasonality, maximum temperature of warmest month, temperature annual range, mean temperature of wettest quarter, annual precipitation, and precipitation of warmest quarter. A random 75% of the presence points were used to develop each model; the remaining 25% were used to test model performance. The final model was chosen using the highest AUC (area under the receiver operating curve; Elith et al. 2006). We used the lowest presence threshold (Pearson et al. 2007) to define climatically suitable areas. Climatic suitability maps for each species were generated in ArcMap where each grid cell had values ranging continuously from 0 (low suitability) to 1 (high suitability) and can be interpreted as the probability of presence of suitable environmental conditions for the target species. The symbology was altered to achieve an appropriate colour representation. The dark areas indicate suitable habitat and the lighter areas represent unsuitable or marginal habitat. The same measured grid of 15 x 15 decimal degrees used for the distribution mapping was overlaid on the map at the same geographic coordinate system. A final map of species richness was compiled indicating the potential species richness in each 15^0 x 15^0 square. A contingency table was constructed in

which naturalization and climate suitability were correlated using the number of countries in which *C. cunninghamiana*, *C. equisetifolia* and/or *C. glauca* have been introduced (Table 2.2). A chi-square test was used to determine significance.

Roughly 8 % of the earth's land area is bioclimatically similar to the native ranges of casuarinas (Fig. 2.3d). *Casuarina* species have been introduced to most parts of the world identified as being climatically suitable. In the introduced range, Central and South America, Southeast and southern Africa, the Caribbean and Southeast Asia are regions of high climatic suitability (Fig. 2.3d). Climate suitability does provide some predictive information of naturalization (chi-square = 8.78, $p<0.05$; Table 2.2).

It is unsurprising that some of the major areas of *Casuarina* invasions, namely Florida and La Réunion Island (see Box 2.1 and 2.2), are predicted to be climatically suitable for *C. cunninghamiana*, *C. equisetifolia* and *C. glauca* (Fig. 2.3c and Fig. S2.1), though these areas are also climatically suitable for an additional four species not yet introduced as far as we know (Fig. 2.3d). South Africa is climatically similar to Australia (Richardson and Thuiller 2007) – the native range of many *Casuarina* species. Five species have been introduced into South Africa in the past (Poynton 1995) and two species are currently naturalized: *C. cunninghamiana* and *C. equisetifolia* (Henderson 2007). Figure S2.1 shows that coastal areas of South Africa are suitable for *C. cunninghamiana*, *C. glauca* and to a lesser extent *C. equisetifolia*. South Africa is also suitable for two other introduced species: *C. cristata* and *C. junghuhniana* (Fig. 2.3d). Given the climatic suitability of South Africa for the above-mentioned species, we can expect further naturalizations in the future. Large plantations of several *Casuarina* species have been established in southern China, India and Taiwan - regions which are climatically suitable for at least six *Casuarina* species (Fig. 2.3d) including the three invasive species (Fig. S2.1). Apart from a few unpublished reports on casuarinas becoming problematic on the Indian coast, it is surprising that few records of naturalization in these countries exist. In Hawaii, *C. cunninghamiana*, *C. equisetifolia* and *C. glauca* are classified as invasive, but Figure S2.1 shows that the island group is only climatically suitable for one invasive species. Large parts of Argentina, Brazil and Southeast Africa are climatically suitable for all three invasive species and given that these species have been introduced to these areas, naturalizations and invasions can be expected in the future. Four countries (Egypt, Japan, Iraq and Israel) in which casuarinas are naturalized, fell outside areas identified as being climatically suitable (Table 2.2). The performance of *C. junghuhniana*

needs to be monitored in countries such as Kenya, Tanzania, Senegal, Uganda, China, India, Taiwan and Thailand where large-scale plantings have been established in climates similar to its native range. Other taxa which, although not yet widely planted, could invade certain habitats include *C. cristata* (Doran and Turnbull 1997) and *C. obesa*. The fact that casuarinas have become naturalized (at least, if not invasive) in many areas where they have been planted for more than 50 years in climatic conditions similar to their native range, suggests that one reason for the lack of reports of naturalization is the short residence time.

2.6 Ecological and economic importance of *Casuarina* and the rationale for introductions

Invasion pathways for woody invasive species are shaped by the demand for the species in the receiving environment (Richardson and Rejmánek 2011). Trees are often cultivated in large numbers, at multiple foci and close to many potentially invasive habitats (Richardson 1998). Cultivated trees are nurtured and protected from disturbance effects, allowing them to attain maturity and accumulate large propagule banks.

The global demand for fast-growing trees increased sharply from the middle of the 19th century when many species were tested and transported around the world (Bennett 2011), e.g. as part of the Empire Forestry movement (Barton 2002). Australian tree species of the genera *Acacia*, *Casuarina* and *Eucalyptus* were well suited to warmer climates and proved to be of substantial economic value (Bennett 2010), and are now prominent features in many landscapes around the world. The selection of a particular species depends on several factors: the climatic conditions in the area, proximity to the sea, wind, soil erosion and soil mineral deficiencies at the plantation sites (Sayed, 2011). At least six *Casuarina* species have been widely introduced and extensively cultivated (Wilson and Johnson 1989; Steane et al. 2003). Historically, casuarinas were planted on relatively poor soils as they grew well where most other tree species did not. They were generally not considered high-value trees, but filled an important ecological niche.

The number of uses for casuarinas continues to increase. Casuarinas, along with acacias and eucalypts, are key taxa where major reforestation programmes are underway or are being considered in many parts of the world. The wood of casuarinas is an important source of firewood and charcoal (Fig. 2.1d) and is often used for general construction purposes (poles, fences, rafters, beams, tool handles etc.) (Fig. 2.1h and l) and other wood-based industries

(veneer for plyboard and woodchips for paper pulp) (Zhong et al. 2010a). Casuarinas are commonly planted for windbreaks (Poynton 1995; Castle 2008) (Fig. 2.1f) and erosion control, particularly along coastlines, sand dunes and river banks (Parrotta 1993). Forbes and Broadhead (2007) and Zhong et al. (2010b) stress the importance of *C. equisetifolia* as shelter trees during typhoons and tsunamis in Asia. In India, vast plantations of *C. equisetifolia* (funded and facilitated by various nongovernment and international organisations like the World Bank) have been established along the coast to act as bioshields. They are grown as ornamental (Fig. 2.1c) and shade trees (Fig. 2.1b) and are often pruned into hedges (Parrotta 1993). They are widely used in agroforestry and for rehabilitation (Fig. 2.1a) and wood production programs (Zhong et al. 2010a). They enhance ecosystem fertility (Diagne et al. 2013) and are therefore valued as pioneer trees for intercropping (Fig. 2.1g), soil improvement and degraded sites due to their N-fixing capabilities and high rates of litter production (Zhong et al. 2010a). The bark of casuarinas is rich in tannin and is used for dyeing leather and fishing nets (Parrotta 1993). The bark and branchlets may have medicinal properties and are used to treat beriberi by some native communities in New Zealand (Parrotta 1993). Although of limited value as a source of fodder, casuarinas are sometimes used for this purpose during times of drought (Doran and Hall 1983).

2.7 Casuarinas as naturalized and invasive alien trees around the world

A number of mechanisms may explain some of the variation in performance of the same invasive species across multiple introductions (Kueffer et al. 2010; 2013). A better understanding of these factors will improve our ability to predict the outcome of *Casuarina* invasions.

Despite the large and growing distribution of the genus outside its native range, very little is known about the invasion ecology of casuarinas. We know of no detailed studies of the invasion ecology of any *Casuarina* species at any site (this is in marked contrast to acacias, eucalypts and pines where invasions have been studied at many sites). *Casuarina* species invade habitats of strongly contrasting characteristics (e.g. beach crests, young volcanic flows, riparian ecosystems) where the requirements for successful invasion are quite different to other tree taxa. In their global review of invasive trees and shrubs around the world, Rejmánek and Richardson (2013) present evidence of three *Casuarina* species being invasive in nine regions around the world. *Casuarina equisetifolia* was noted as being invasive in North America (Florida) (Fig. 2.2f), Asia, Southern Africa (Fig. 2.2i), Central America and

South America. *Casuarina equisetifolia* is considered invasive on the following islands: Ascension, Bermuda, Canary Islands, Cayman Islands (Fig. 2.2h), Dominican Republic, Hawaii, Jamaica, La Réunion (Fig. 2.2d), Ogasawara, Puerto Rico, Seychelles (cf. Kueffer et al. 2010). *Casuarina cunninghamiana* was noted as invasive in southern Africa and La Réunion Island (Box 2.2). *Casuarina glauca* was listed as invasive in North America (Florida) and the Pacific Islands (Hawaii) (Figs 1.2b, c and g), and recorded as a potential invader in Madagascar. *Casuarina equisetifolia* is the most widely planted species in the genus and also the most invasive.

We use different case studies from key *Casuarina* invasions around the world (see Box 2.1 and 2.2). These case studies serve as a tool for facilitating the development of screening models for given systems by providing useful insight into the rationale behind human-mediated introductions, impacts on different ecosystems and management approaches adopted in different parts of the world for a globally important group of plants. In these case studies, casuarinas were introduced into different environments, at different times, for different purposes where various human and environmental disturbances have facilitated establishment. Perceptions of casuarinas, stages in the introduction-naturalisation-invasion continuum, the impacts associated with invasion, and management efforts differ markedly in each region. Comparable conflicts of interest exist in each region as the benefits of casuarinas are weighted against the costs.

2.8 The expanding global range of *Casuarina*

As with Australian acacias (Richardson et al. 2011), not all *Casuarina* species have been moved out their native ranges to the same extent over the same periods, and some have not been moved at all. This complicates the task of separating human factors from biological mechanisms as mediators of invasion success. In this section we quantify the importance of casuarinas around the world and explore the link between native range size and naturalized success.

2.8.1 The importance of casuarinas globally

To derive a rough measure of the relative importance of *Casuarina* species in different parts of the world, we ran a search for "casuarina" in the CAB Abstracts Database for the period 1966-2012 (3 August 2012; http://www.cabi.org/) (CAB International, Wallingford, Oxford, UK). The CAB Abstracts Database has been shown to be a useful source of information for

deriving a rough measure of the global distribution of tree species with commercial value, e.g. for *Pinus* (Richardson et al. 1994; Procheş et al. 2012). Each abstract was manually searched and the location for each species recorded. The *Casuarina* species in Table S2.2 are those that have been introduced around the world and propagated to various degrees by humans. Some (but not all) species are commercially important. For a more detailed dataset, see Table S2.3.

Figure 2.4 shows the number of countries into which casuarinas were introduced at various times. Eight species (and one hybrid) in the genus have been widely introduced around the world and three have become naturalized/invasive in many countries. These three species are the most widely introduced, and *C. cunninghamiana* has experienced the greatest introduction effort. Most introductions took place between 1950 and 2000 – too recently for widespread invasions to have been reported. This points to a substantial invasion debt.

2.8.2 The relationship between the native range and the naturalized success

A positive relationship between the size of the native range and the likelihood of becoming invasive has been demonstrated for many plant taxa, including Australian tree taxa (Hui et al. 2011). In addition, tolerance of a wide range of climates in the region of origin is an important determinant of invasiveness for a species (Pyšek et al. 2009b). Several studies have also shown a strong positive relationship between the extent of human usage and the adventive range of alien plants (Wilson et al. 2007; Castro-Díez et al. 2011). We were interested to determine the relationship between native range size for *Casuarina* species and the extent of introductions around the world, naturalized range size and extent of invasiveness.

We tested the relationship between native and naturalized range size using a Spearman's rank correlation for all species (Fig. 2.5a). *Casuarina equisetifolia, C. cunninghamiana* and *C. glauca* are naturalized in 32, 13 and 6 countries respectively (36 countries in total). There is a positive correlation between native and naturalized range sizes ($r = 0.84$; $p<0.005$). A large native range size is strongly associated with naturalization (Fig. 2.5a). While this is in line with the link between invasiveness and range size, it is not clear what the mechanisms are. However, human interest in a given taxon may explain much of the variation in the extent of naturalization (Table S2.2). This is in agreement with other recent studies (Pyšek et al. 2009a; Procheş et al. 2012).

We plotted the frequency of citations in the forestry literature (as a crude proxy for planting intensity; see above) against native range size and naturalized range size (Fig. 2.5b) of all *Casuarina* species. Note that a strong bias exists in favour of data for developed countries. Naturalized species tend to have greater coverage in the literature (Fig. 2.5b) than species that have not become naturalized. Of those that are naturalized, those with more citations in forestry abstracts in the CAB Forestry Compendium tended to have larger naturalized ranges (Fig. 2.5b). The number of citations in both the naturalized and native range sizes was similar for the three invasive species (Fig. 2.5b). However, despite the native range size and global introduction effort of some of the remaining species, no naturalization is observed (Fig. 2.5a and b). The three invasive species are better studied and consequently have more references, as they have larger native ranges (Fig. 2.5b). It should be noted that many areas where the three invasive species are known to be naturalized (references in other databases), were not referenced in the forestry abstracts and are consequently underrepresented (Fig. 2.5b). There were no citations for *C. orophila, C. potamophila, C. tenella and C. teres.*

2.9 Do certain life-history traits make some *Casuarina* taxa more invasive?

Understanding whether successful invaders possess a distinct set of life-history traits is important for the prediction and management of future invaders (Hamilton et al. 2005). We explore whether certain life-history traits (Table 2.3) predispose some casuarinas to become naturalized in their new ranges.

Human-mediated dissemination of important species to and within new regions increases the risk of invasion (Castro-Díez et al. 2011). Traits associated with the ecological performance of a species (and consequently potential invasiveness) in new environments are closely related to traits associated with human use (Castro-Diez et al. 2011; Richardson et al. 2011). This complicates attempts to explain the extent of naturalization/invasion of introduced species, since patterns of invasion may simply reflect levels of introduction effort and propagule pressure which may mask potentially important roles of other factors. High levels of propagule pressure as a result of planting, inevitably lead to the escape of woody species from cultivation, irrespective of biological traits (Pyšek et al. 2009a).

As is the case with Australian acacias (Richardson et al. 2011), accurate data on most traits is only available for a sample of *Casuarina* species – generally only those species that are most useful to humans. Consequently, correlating performance as introduced species with traits

across the full spectrum of species is difficult. The same traits that allow a species to be widespread in the native range should contribute to their ability to overcome abiotic filters and successfully establish in a new region (Schaepfer et al. 2010). Differences in a few key traits between closely-related species can promote invasiveness (Funk et al. 2008).

Casuarinas possess a range of traits that make them popular as multipurpose trees, but the same traits also enhance their invasive capacity and their ability to cause impacts in invaded ecosystems. Such traits include: rapid growth; a tolerance of high salinity, cold temperatures, low soil fertility and arid conditions; the capacity to establish and propagate easily; the ability to coppice; and the production of dense wood (Table 2.3). Symbiotic associations with N-fixing actinobacteria from the genus *Frankia* as well as ecto-, endo- and arbuscular mycorrhizal fungi allow them to grow in and enrich degraded and waste land soil (Diagne et al. 2013). Their enormous reproductive capacity (hundreds of cones per tree each consisting of 40-60 winged seeds), ability to rapidly colonize disturbed/open habitats, short juvenile period, and their ability to grow well at high densities make them useful for many purposes (Rockwood and Geary 1991) but also contribute to their weediness.

Rejmánek and Richardson (2006) showed that life-history traits clearly separate invasive from non-invasive *Pinus* species. However, no life-history traits (or suite of traits) clearly separate invasive from non-invasive *Casuarina* species (Table 2.3). Native range size and the level of dissemination and propagule pressure resulting from human usage seem to be much better predictors of invasiveness and invasion success of casuarinas than any single trait or combination of traits.

2.10 Ecological factors that potentially influence the invasion ecology of casuarinas

Key traits and/or trait combinations of economically and ecologically important tree species are associated with their roles as early-seral plants (Strauss and Ledig 1985) and potential invaders (Richardson 1989). Here, we discuss some important ecological factors that contribute to the invasive success of casuarinas. Most of these factors have not been studied in the context of invasion ecology and further work is needed.

2.10.1 Symbiotic associations

Alien plant and microbe mutualists can facilitate each other's spread as they co-invade new ranges (Porter et al. 2011). Casuarinas form symbiotic N-fixing associations with soil

actinomycetes from the genus *Frankia* as well as ecto-, endo- and arbuscular mycorrhizal fungi (Zhong et al. 1995; Wang and Qiu, 2006). These symbiotic associations allow casuarinas to fix nitrogen at rates similar to nodulated legumes (Zhong 1993). As for Australian acacias (Morris et al. 2011), N-fixation can result in alteration of soil-nutrient cycling and enrichment of soil N which hinders the competitive ability of native species. N-fixing species have been shown to severely alter ecosystem function (Vitousek and Walker 1989). This may relate to the empty niche hypothesis as N-fixing species may be particularly problematic on islands as they fill an empty niche (Vitousek and Walker 1989).

The association of *Casuarina* roots with both types of mycorrhizae significantly enhances the adaptability of these species and their ability to grow in harsh environments. Specifically, the fungi help the trees by: improving mineral nutrition (increasing availability of phosphorus and increase absorption of soil nitrogen) (Elumalai and Raaman, 2009; Zhong et al., 2010); increasing tolerance to drought (Zhang et al. 2010), flooding (Osundina, 1997) and salt stress (Evelin et al. 2009); influencing the N-fixing ability of *Frankia* (He and Critchley 2008); improving soil structure (hyphal mats contribute to soil binding); increase disease resistance (by preventing access of the pathogen to the plant root) (Liu et al. 2007; Sayeed and Siddiqui 2008); alleviating the effects of acid soils (Diem et al. 2000). *Casuarina* roots also interact with unidentified soil microorganisms that cause the development of proteoid roots (Diem et al. 2000). These roots appear to greatly increase the surface area for nutrient absorption, however little is known about their benefits. These associations help casuarinas to occupy nitrogen-poor sites such as coastal dunes and disturbed areas. A study in Senegal showed that the amount of soil nitrogen under *Casuarina* trees increased by 58 kg ha^{-1} yr^{-1} to nearby sand dunes without casuarinas (U.S. National Research Council, 1984). This partly explains the popularity of casuarinas for dune stabilization, land reclamation, intercropping and agroforestry (Zhong et al. 1995). The rate of N-fixation is species-dependant and also differs according to environmental factors and the strain of the *Frankia* symbiont (U.S. National Research Council 1984). While certain *Casuarina* species may combine mycorrhizae and N-fixing nodules in some areas, these mutualisms may be mutually exclusive in others (Orians and Milewski 2007). Richardson et al. (2000) suggested that co-invasion by specific strains of *Frankia* is critical to the success of casuarinas, but this has not been verified.

2.10.2 Hybridization

Hybridisation in plants allows for an increase in genetic variation and production of novel

gene combinations, potentially fuelling the evolution of invasiveness (Gaskin et al. 2009). Interspecific hybridization, which may contribute to the success of invasive species (Ellstrand and Schierenbeck 2000), occurs among casuarinas (Wheeler et al. 2011) making species' identification difficult (Ho et al. 2002). *Casuarina equisetifolia* is monoecious and is therefore well adapted to propagate itself as individual plants easily self-seed (Castle et al. 2008). Thus, the likelihood of interspecific hybridization is significantly higher when in close contact with other species (Castle et al. 2008). *Casuarina glauca* and *C. cunninghamiana* are dioecious suggesting that male and female plants would need to be in close proximity to one another in order to produce hybrid seeds (Castle et al. 2008). Gaskin et al. (2009) reported hybrids between *C. equisetifolia* and *C. glauca* and possibly between *C. glauca* and *C. cunninghamiana* in Florida. Even though the native ranges of these species overlap, Gaskin et al. (2009) detected no hybridization in Australia. In Egypt, several hybrids (e.g. the natural hybrid *C. cunninghamiana* × *C. glauca*) have been selected for improved biomass production under a range of environmental conditions (El-Lakany 1983). Ho et al. (2002; 2011) suggest that cultivated casuarinas in Taiwan are the result of introgressive hybridization involving *C. equisetifolia*, *C. glauca*, and possibly *C. cunninghamiana*. Their results also imply that most casuarinas in Taiwan are derived from the backcrossing to *C. equisetifolia*. In addition, Ndoye et al. (2011) suggested that cultivated populations of *C. equisetifolia* in Senegal are subject to hybridization and inbreeding depression. Chen and Li (2002) showed that very high inbreeding retrogression occurred in a *C. equisetifolia* plantation on the southeast coast of the People's Republic of China, indicating that inbreeding and its subsequent retrogression played an important role in the decline of the plantation. A hybrid of *C. junghuhniana* and *C. equisetifolia* was brought to India from Thailand as fuel for the tea-drying industry (U.S. National Research Council 1984). The role of these novel hybrids in the success of these invasive species has not yet been investigated.

In Florida, a proposal was put forward for a licensed nursery to provide only male plants for establishment around citrus groves and in addition, include a tax per tree which would supply funding for the control of *C. equisetifolia* and/or *C. glauca*. Growers would obtain permits from the Department of Environmental Protection (DEP) (as opposed to delisting the species) as casuarinas are prohibited. However, members of the Florida Exotic Pest Plant Council (FLEPPC) were concerned that introgression may become problematic as male trees present a large reservoir for hybridization. Novel *Casuarina* hybrids in Florida have no co-evolutionary history with any insects or diseases, which may be problematic for biological control efforts

(Gaskin et al. 2009). Although fully sterile cultivars may alleviate any hybridization concerns, they would take time to develop and this does not resolve the biocontrol conflict. Castle (2008) provides a useful identification key for the three invasive *Casuarina* species.

2.11 Impacts of casuarinas in their new ranges

Casuarinas are early-successional and fast-growing species of extreme abiotic conditions (sandy, nutrient-poor soils, and tolerance of extreme fluctuations of soil water from very dry to inundated). They are able to tolerate sites with relatively high salinity, low soil fertility and arid conditions. As a result, open, sandy habitats particularly along coastlines in which disturbances have occurred, are particularly susceptible to invasion. These trees have an enormous reproductive capacity due to wind-dispersed seeds that germinate easily to form dense seedling banks and eventually monotypic stands (Kueffer and Lavergne 2004; Wheeler et al. 2011). The habitats of invaded areas are dramatically altered as native plants are overwhelmed by the rapid growth, dense coverage, and thick litter accumulation (Hammerton 2001). Dense shade combined with allelochemical leachates result in a reduction in germination and establishment of native vegetation (Smith 1998; Weber 2003) – providing support for the novel weapons hypothesis (Lamarque et al. 2011). Casuarinas also promote coastal erosion as their shallow roots and tall canopies result in trees being blown over during hurricanes (Austin 1978; Deaton 1994; Swearingen 1997; Hammerton 2001; Sealey 2006). They are known to reduce small mammal populations (Mazzotti et al. 1981) and interfere with the nesting of beach-dwelling reptiles such as the loggerhead and green sea turtles, and the American crocodile (Klukas 1969; Doren and Jones 1997). Large-scale plantations of *C. equisetifolia* established on the coast of India negatively impact the nesting of olive ridley turtles along the Northern Tamil Nadu Coast (Chaudhari et al. 2009). Subramanean and Reddy (2010) revealed that the average population abundance of the sand skink (*Eutropis bibronii*) on the coast of India was significantly reduced by *C. equisetifolia* plantations. Massive plantations may also restrict sand dune formation - an integral part of seashore topography and beach ecosystems (Chaudhari et al. 2009). Snyder (1992) reports that the dense roots of casuarinas reduce soil moisture and damage drains, piping and paving. *Casuarina equisetifolia* has been shown to reduce insect species richness and alter species composition (Sugiura et al. 2012). A recent study conducted by Hata et al. (2012) on Chichijima Island in the subtropical Ogasawara (Bonin) Islands showed that litter

decomposition of *C. equisetifolia* may alter the total N and N-cycling in invaded forest ecosystems.

2.12 *Casuarina* as a model group

Information summarized in this paper shows that casuarinas share similar drivers of invasion success with other important model groups of woody plants such as Australian acacias, *Eucalyptus* and *Pinus*. The link between planting intensity and degree of invasion in casuarinas resembles that of Australian acacias and eucalypts. As with Australian acacias (Castro-Díez et al. 2011) and eucalypts (Rejmánek et al. 2005), but unlike pines (Richardson et al. 1994), propagule pressure explains much more of the variance in observed invasiveness between *Casuarina* taxa than any known combination of life-history traits. Like Australian acacias (Hui et al. 2011), *Casuarina* species with large native ranges are most likely to be introduced and become naturalized (Fig. 2.4a). As with Australian acacias and eucalypts, casuarinas exhibit little trait variation and similar traits are shared with each of these model groups, enhancing their capacity to invade (Table 2.3). These include: symbiotic associations; fast growth; the ability to grow on low nutrient, highly disturbed soils; intra-specific hybridization between mixed genetic entities in the invasive range. As is the case with alien trees of other taxa (e.g. Kull et al. 2011 for Australian acacias), the number of uses for casuarinas is continuously increasing while the perceptions of alien *Casuarina* species by human societies differ markedly between regions of the world, which in some cases has led to complex conflicts of interest (Box 2.1 and 2.2). Importantly, casuarinas differ from other model groups in that they invade habitats not invaded by most other invasive woody plants - making this group functionally unique.

2.13 Evolution of management approaches for invasive casuarinas

Trees introduced around the world for forestry and agroforestry are predominantly selected for their rapid growth, tolerance of a wide range of conditions, and abundant fruiting and/or seed production (Richardson et al. 2004). These factors can also influence the likelihood of future problems with invasive trees, and so need to be explicitly considered in management schemes (Richardson and Rejmánek 2011).

A range of control methods have been proposed to manage invasive *Casuarina* species. In Florida (USA), Hammerton (2001) and Weber (2003) found fire to be effective for the control of *C. equisetifolia* and *C. glauca*, but only in areas of high density under dry

conditions. The trees have some protection from high-intensity fires as understorey vegetation is generally minimal (Smith 1998). *Casuarina equisetifolia* has been noted to recover partially after fire from the basal roots, although the coppicing ability of this species is poorer than for species such as *C. glauca* (Smith 1998). To reduce opportunities for the colonization of *C. equisetifolia*, Swearingen (1997) and Weber (2003) recommend the immediate removal of fallen leaves, cones, seeds and saplings. To avoid the spread of *C. cunninghamiana* along watercourses, Merwin (1989) suggests avoiding planting along riparian corridors. Elfers (1988) and Swearingen (1997) suggest that habitat disturbance should be minimized to reduce opportunities for *Casuarina* colonization and when habitats are disturbed, immediate replanting with native vegetation is required. Control efforts that target the reproductive structures and saplings could reduce the spread of casuarinas into natural areas without affecting their horticultural value. Pemberton (1996) suggests *C. equisetifolia* to be an excellent candidate for biological control because of its large native range, number of congeners, and known enemies. Control methods have been hampered by conflicts of interest regarding perceived uses (see Box 2.1). For example, on Sanibel Island off the coast of Florida, efforts to remove monotypic stands of casuarinas to re-establish native plant communities and wildlife habitats have been met with intense emotional resistance, including death threats to land managers (Loflin 2004).

In South Africa, *C. cunninghamiana* and *C. equisetifolia* are declared as Category 2 invaders by the Conservation of Agricultural Resources Act, 1983 (Henderson 2001; Henderson 2006). This means that a demarcation permit is required to import, possess, grow, breed, move, sell, and buy the species. Also, no permits are issued for planting of casuarinas in riparian zones. In the Cayman Islands, an immediate importation ban has been implemented for *C. equisetifolia* where control methods, feasibility studies and cost analyses are to be conducted to determine the most appropriate management options for this species. Remote sensing techniques are soon to be implemented to help assess the impact and spread/control of *C. equisetifolia* in the Cayman Islands. Wheeler et al. (2011) propose that the most cost-effective and sustainable management method of casuarinas in Florida lies in a comprehensive integrated control strategy involving safe biological control as a major priority. This management method not only decreases pesticide exposure to humans but can be highly effective (Nel et al. 2004).

Management should be addressed through an ecosystem approach whereby holistic decision-making is implemented. The spatial dimensions of ecological and evolutionary processes or future land-use pressures need to be addressed before conservation planning commences. An assessment of conservation priorities for each region is required. Stakeholder engagement and communication, monitoring, and adaptive management are needed. The solution to problems caused by casuarinas lies in integrating various control methods

2.14 Priorities for future research

Work is needed to improve our understanding of the global distribution of the genus, taxonomic issues, and the many dimensions of interactions between casuarinas and biotic and abiotic factors in their new ranges that are required to develop a robust and predictive understanding of the invasion ecology of the group. We need to understand the importance of mutualisms between *Casuarina* species and soil biota in mediating naturalization, invasion and impacts. Further research is needed to determine the extent of hybridization in the native and adventive ranges of the genus, and the potential role of this factor in mediating invasions. Our review has shown the importance of macroclimate in *Casuarina* invasions (Fig. 2.3d; Fig. S2.1) – all major invasions of casuarinas have occurred in regions with similar climatic conditions to those that exist in the native range of the genus. Further work to determine microclimatic and microsite requirements of different taxa may well shed light on why certain species have not become widely naturalized or invasive in some areas. The structure and functioning of biological systems both influence and are influenced by the balance of carbon: nitrogen: phosphorus (C: N: P) ratios between organisms and their environment (González et al. 2010). The ecological stoichiometry of invasive organisms across gradients of nutrient availability remains largely unexplored. As ecosystem resource availability, organism nutrient requirements, and individual competitiveness for resources may be the main interacting mechanisms explaining invasion success, it would be interesting to determine whether C: N: P stoichiometry constrains key physiological and ecological processes, ultimately predicting invasion success in casuarinas.

Various approaches for managing invasive casuarinas have been tried in different parts of the world. Successes and failures need to be comprehensively reviewed to compile guidelines for best-management practices in different situations. Different environmental and socio-political situations produce different categories of conflicts of interest and useful approaches for dealing with these are emerging following trial and error in different settings. Again,

lessons must be learnt and guidelines for innovative solutions need to be compiled. Biological control holds much promise.

2.15 Conclusions

Casuarinas have been widely planted by different stakeholders for a variety of reasons, but rarely for commercial purposes. They exhibit similar behaviour to other model groups of trees. For example, like Australian acacias and eucalypts, the extent of invasions is positively correlated with the native range size of *Casuarina* taxa. Invasion success is strongly linked with propagule pressure (as reflected in crude proxies such as coverage in the forestry literature). Like Australian acacias, but unlike pines, they show very little trait variation, and invasiveness cannot be explained on the basis of life-history traits. Casuarinas differ by invading different habitats to most other invasive woody plants (e.g. acacias, eucalypts and pines). A range of management approaches have been tried with varying levels of success in different parts of the world. A substantial invasion debt exists and attention must be devoted to planning to deal with new invasions that will arise in many parts of the world. As with other model groups (e.g. Wilson et al. 2011), lessons can be learnt from regions with a longer history of introduced casuarinas.

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References

Austin DF (1978) Exotic plants and their effects in Southeastern Florida. Environ Conserv 5:25–34

Baret S, Rouget M, Richardson DM, Lavergne C, Egoh B, Dupont J, Strasberg D (2006) Current distribution and potential extent of the most invasive alien plant species on La Réunion (Indian Ocean, Mascarene Islands). Austral Ecol 31:747-758

Barton GA (2002) Empire forestry and the origins of environmentalism. Cambridge University Press, Cambridge

Bennett BM (2010) A global history of Australian trees. J Hist Biol 44(1):125-145

Bennett BM (2011) Naturalizing Australian Trees in South Africa: Climate, exotics and experimentation. J Sth Afr Stud 37:225-280

Blake A (2009) Protecting swamp sheoke: an endangered species of Victoria's Wimmera Woodlands. Australas Plant Conserv 18:14-15

Blombery AM (1977) Australian Native Plants. Angus and Robertson Publishers, Melbourne

Boland DJ, Brooker MIH, Chippendale GM, Hall N, Hyland BPM, Johnston RD, Kleinig DA, Turner JD (1984) Forest Trees of Australia: Over 200 of Australia's Most Important Native Trees Described and Illustrated. Nelson Wadsworth, Melbourne

Boland DJ, Moncur MW, Pinyopusarerk K (1996) Review of some floral and vegetative aspects to consider when domesticating *Casuarina*. Proc. Third Int. *Casuarina* Workshop, CSIRO, Australia, pp 17-25

Bourke RM (1985) Food, coffee and casuarina: an agroforestry system from the Papua New Guinea highlands. Agroforest Syst 2(4):273-279

CAB International (2000) Forestry compendium global module. Wallingford, UK, CAB International

Castle WS (2008) Field guide to identify the common *Casuarina* (Australian pine) species in Florida. Univ Fla Coop Extension Serv Publ HS 1140

Castle WS, Langeland KA, Rockwood DL (2008) *Casuarina cunninghamiana* Miq. (River sheoak) in Florida and its potential as a windbreak plant for citrus groves. Extension Digital Information Source (EDIS), Horticultural Sciences Department, University of Florida, Gainesville. http://edis.ifas.ufl.edu/pdffiles/HS/HS39200.pdf. Accessed 27 March 2012

Castro-Díez P, Godoy O, Saldaña A, Richardson DM (2011) Predicting invasiveness of Australian acacias on the basis of their native climatic affinities, life history traits and human use. Divers Distrib 17:934–945

Chapman TF (2007) Foods of the glossy Black-Cockatoo *Calyptorhynchus lathami*. Aust Field Ornithol 24:30–36

Chaudhari S, Devi Prasad KV, Shanker K (2009) Impact of *Casuarina* Plantations on Olive Ridley Turtle Nesting along the Northern Tamil Nadu Coast, India. ATREE, Bangalore and MCBT, Mamallapuram, India, pp 44

Cheke A, Hume J (2008) Lost land of the Dodo: an ecological history of the Mascarene Islands. T and AD Poyser, London

Chen X, Li P (2002) Mating system and inbreeding retrogression of Casuarina equisetifolia plantation, an introduced species in Xiamen. Ying Yong Sheng Tai Xue Bao 13:1377-1380

Chezhian P, Yasodha R, Ghosh M (2009) Genetic Diversity Analysis in *Casuarina* and *Allocasuarina* Species Using ISSR Markers. *Madras Agric J* 96(1-6):32-39

Comer CW, Conde LF, Rockwood DL, Geary TF (1986) *Casuarina* cultural improvement in Florida. Nitrogen Fixing Trees Research Report 4:53

CSIRO (2011) Biological control of Australian native Casuarina species in the USA. http://www.csiro.au/en/Outcomes/Food-and-Agriculture/Biological-control-of-Australian-native-Casuarina-species-in-the-USA.aspx. Accessed 10 October 2012

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

Deaton A (1994) Shoreline monitoring at Long Key. Resource Manage Notes 6:13–14

Diagne N, Diouf D, Svistoonoff S, Kane A, Noba K, Franche C, Bogusz D, Duponnois R (2013) *Casuarina* in Africa: Distribution, role and importance of arbuscular mycorrhizal, ectomycorrhizal fungi and *Frankia* on plant development. J Environ Manage 128:204-209

Diem HG, Duhoux E, Zaid H, Arahou M (2000) Cluster roots in Casuarinaceae: Role and relationship to soil nutrient factors. Ann Bot 85:929-936

Dogra KS, Sood SK, Dobhal PK, Sharma S (2010) Alien plant invasion and their impact on native species diversity at global scale: a review. J Ecol Nat Environ 2(9):175-186

Doran JC, Turnbull JW (1997) Australian trees and shrubs: species for land rehabilitation and farm planting in the tropics. ACIAR Monograph No. 24. Australian Centre for International Agricultural Research, Canberra

Doren RF, Jones DT (1997) Plant management in Everglades National Park. In: Simberloff D, Schmitz DC, Brown TC (eds) Strangers in Paradise: Impact and Management of Nonnative Species in Florida. Island Press, Washington, D.C., pp 275-286

Elevitch CR (ed.) (2006) Traditional Trees of Pacific Islands: Their Culture, Environment, and Use. Permanent Agriculture Resources, Holualoa, Hawaii

Elfers SC (1988) Element Stewardship Abstract for *Casuarina equisetifolia*. Report to The Nature Conservancy, 14 p. On file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Fire Sciences Laboratory, Missoula

Elith J et al (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecogr 29:129–151

El-Lakany M (1996) A brief account of *Casuarina* research: past achievements and future trends. Proc. 3rd Int. *Casuarina* Workshop, CSIRO, Australia, pp 12-16

Ellstrand NC, Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? Proc Nat Acad Sci USA 97:7043-7050

Elumalai S, Raaman N (2009) In vitro synthesis of *Frankia* and mycorrhiza with *Casuarina equisetifolia* and ultrastructure of root system. Indian J Exp Biol 47:289-297

Emmott T, Greening Western Australia (2001) Swamp Sheoak (*Casuarina obesa*) use in farm forestry. http://www.avongro.com.au/Webpages/documents/GAWASwampSheoak.pdf. Accessed 10 June 2012

ESRI (2010) ArcGIS Desktop. Redlands, CA, USA

Evelin H, Kapoor R, Giri B (2009) AMF in alleviation of salt stress: a review. Ann Bot 104:1263-1280

Feagin RA, Mukherjee N, Shanker K, Baird AH, Cinner J, Kerr AM, Koedam N, Sridhar A, Arthur R, Jayatissa LP, Lo Seen D, Menon M, Rodriguez S, Shamsuddoha M, Dahdouh-Guebas F (2010) Shelter from the storm? Use and misuse of coastal vegetation bioshields for managing natural disasters. Conserv Lett 3:1–11

Flannery T (1999) The Birth of Sydney. Grove Press, New York

FLEPPC (Florida Exotic Pest Plant Council) (2010) Florida Exotic Pest Plant Council Invasive Plant Lists. www.fleppc.org. Accessed 28 February 2010

Forbes K, Broadhead J (2007) The Role of Coastal Forests in the Mitigation of Tsunami Impacts. FAO Regional Office for Asia and the Pacific Publication 2007. http://www.fao.org/forestry/media/14561/1/0/. Accessed on 20 June 2012

Funk JL et al (2008) Restoration through reassembly: plant traits and invasion resistance. Trends Ecol Evol 23:695–703

Gallagher RV, Leishman MR, Miller JT, Hui C, Richardson DM, Suda J, Trávníček P (2011) Invasiveness in introduced Australian acacias: the role of species traits and genome size. Divers Distrib 17:884–897

Gaskin JF, Wheeler GS, Purcell MF, Taylor GS (2009) Molecular evidence of hybridization in Florida's she-oak (*Casuarina* spp.) invasion. Mol Ecol 18:3216–3226

Gauthier D, Jaffre T, Prin Y (1999) Occurrence of both Casuarina-infective and Elaeagnus-infective *Frankia* strains within actinorhizae of *Casuarina collina*, endemic to New Caledonia. Eur J Soil Biol 35(1):9-15

GBIF (2008) Global Biodiversity Information Facility (GBIF) Work Programme 2009–2010. Available: http://www2.gbif.org/WP2009-10.pdf. Accessed 21 February 2012

Geary TF (1983) Casuarinas in Florida (USA) and some Caribbean Islands. In: Midgley SJ, Turnbull JW, Johnston RD (eds) *Casuarina* Ecology Management and Utilization. Proceedings of an International Workshop, Canberra, Australia. CSIRO Publishing, pp 107–109

González AL, Kominoski JS, Danger M, Ishida S, Iwai N, Rubach A (2010) Can ecological stoichiometry help explain patterns of biological invasions? Oikos 119:779–790

Gordon DR (1998) Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecol Appl 8:975–989

Griffin AR, Midgley SJ, Bush D, Cunningham PJ, Rinaudo AT (2011) Global uses of Australian acacias recent trends and future prospects. Divers Distrib 17:837–847

Halliday J (1984) Catalogue of nitrogen-fixing tree germplasm. United States Agency for International Development, Hawaii

Hamilton MA, Murray BR, Cadotte MW, Hose GC, Baker AC, Harris CJ, Licari D (2005) Life-history correlates of plant invasiveness at regional and continental scales. Ecol Lett 8:1066–1074

Hammerton J (2001) Casuarinas in the Bahamas: a clear and present danger. Bahamas J Sci 9:2–14

Hata K, Kato H, Kachi N (2012) Leaf litter of the invasive *Casuarina equisetifolia* decomposes at the same rate as that of native woody species on oceanic islands but releases more nitrogen. Weed Res 52:542–550

Henderson L (2001) Alien Weeds and Invasive Plants. Plant Protection Research Institute Handbook No. 12. Agricultural Research Council, Pretoria

Henderson L (2006) Comparisons of invasive plants in southern Africa originating from southern temperate, northern temperate and tropical regions. Bothalia 36:201–222

Henderson L (2007) Invasive, naturalized and casual alien plants in southern Africa: a summary based on the Southern African Plant Invaders Atlas (SAPIA). Bothalia 37:215–248

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J of Climatol 25:1965–1978

Ho K-Y, Lee S-C (2011) ISSR-based genetic diversity of *Casuarina* spp. In coastal windbreaks of Taiwan. Afr J Agric Res 6(25):5664-5671

Ho K-Y, Yang JC, Hsiao JY (2002) An assessment of genetic diversity and documentation of hybridization of *Casuarina* grown in Taiwan using RAPD markers. Int J Plant Sci 163:831–836

Hui C, Richardson DM, Robertson MP, et al. (2011) Macroecology meets invasion ecology: linking native distribution of Australian acacias to invasiveness. Divers Distrib 17:872-883

Hulme PE (2012) Weed risk assessment: a way forward or a waste of time? J Appl Ecol 49(1):10-19

Jayaraj RSC (2010) *Casuarina junghuhniana* (Casuarinaceae) in India. *Aust J Bot* 58(2):149–156

Johnson LAS (1982) Notes on Casuarinaceae II. J Adel Bot Gard 6:73-87

Joseph L (1982) The Red-tailed Black-Cockatoo in south-eastern Australia. Emu 82:42–45

Kalwij JM (2012) Review of 'The Plant List, a working list of all plant species'. J Veg Sci 23: 998–1002

Karimi A, Khodaverdiloo H, Sepehri M, Sadaghiani M (2011) AMF and heavy metal contaminated soils. Afr J Microbiol Res 5:1571-1576

Klukas RW (1969) Exotic terrestrial plants in South Florida with emphasis on Australian pine (*Casuarina equisetifolia*). Homestead, Florida: Everglades National Park. Report No. 33030

Kueffer C et al (2009) A global comparison of plant invasions on oceanic islands. Perspect Plant Ecol Evol Systematics 12: 145-161

Kueffer C, Lavergne C (2004) Case studies on the status of invasive woody plant species in the Western Indian Ocean. 4. Réunion. Forestry Department, Food and Agriculture Organization of the United Nations, Rome, Italy

Kueffer C, Mauremootoo J (2004) Case Studies on the Status of Invasive Woody Plant Species in the Western Indian Ocean. 3. Mauritius (Islands of Mauritius and Rodrigues). Forest Health and Biosecurity Working Papers FBS/4-3E. Forestry Department, Food and Agriculture Organization of the United Nations (FAO), Rome, Italy

Kueffer C, Pyšek P, Richardson DM (2013) Integrative invasion science: model systems, multi-site studies, focused meta-analysis, and invasion syndromes. New Phytol (in press) doi: 10.1111/nph.12415.

Kueffer C, Vos P (2004) Case studies on the status of invasive woody plant species in the Western Indian Ocean: 5. Seychelles. Forest Health and Biosecurity Working Papers FBS/4-5E. Forestry Department, Food and Agriculture Organization of the United Nations, Rome, Italy

Kueffer C et al (2010) A global comparison of plant invasions on oceanic islands. Perspect Plant Ecol 12:145–161

Kull CA, Shackleton CM, Cunningham PS, Ducatillon C, Dufour Dror J-M, Esler KJ, Friday JB, Gouveia AC, Griffin AR, Marchante EM, Midgley SJ, Pauchard A, Rangan H, Richardson DM, Rinaudo T, Tassin J, Urgenson LS, von Maltitz GP, Zenni RD, Zylstra MJ (2011) Adoption, use, and perception of Australian acacias around the world. Divers Distrib 17:822-836

Le Roux JJ, Brown G, Byrne M, Ndlovu J, Richardson DM, Thompson GD, Wilson JRU (2011) Phylogeographic consequences of different introduction histories of invasive Australian *Acacia* species and *Paraserianthes lophantha* (Fabaceae) in South Africa. Divers Distrib 17:861–871

Lamarque LJ, Delzon S, Lortie CJ (2011) Tree invasions: a comparative test for the dominant hypotheses and functional traits. Biol Invasions 13:1969–1989

Langeland KA, Ferrell JA, Sellers B, MacDonald GE, Stocker RK (2011) Integrated management of non-native plants in natural areas of Florida. Gainseville, FL: Institute of Food and Agricultural Sciences, University of Florida. SP 242

Liu J, Maldonado-Mendoza I, Lopez-Meyer M, Cheung F, Town CD, Harrison MJ (2007) Arbuscular mycorrhizal symbiosis is accompanied by local and systemic alterations in gene expression and an increase in disease resistance in the shoots. Plant J 50:529-544

Loflin RK (2004) Letter to the Editor. Southeast Exotic Pest Plant Council (SE-EPPC), Winter 2004

Macdonald IAW, Thébaud C, Strahm WA, Strasberg D (1991) Effects of alien plant invasions on native vegetation remnants on La Réunion (Mascarene islands, Indian Ocean). Environ Conserv 18:51–61

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Marcar N, Crawford D (1995) Trees for Saltland: A guide to selecting native species for Australia, CSIRO Press, Melbourne

Mazzotti FJ, Ostrenko W, Smith AT (1981) Effects of the exotic plants *Melaleuca quinquenervia* and *Casuarina equisetifolia* on small mammal populations in the eastern Florida Everglades. Florida Sci 44:65–71

McNeely JA (ed) (2001) The great reshuffling: the human dimension of invasive alien species. IUCN, Gland, Switzerland

Menkhorst P, Schedvin N, Geering D (1999) Regent Honeyeater (*Xanthomyza phrygia*) Recovery Plan 1999-2003. Department of the Environment, Water, Heritage and the Arts, Melbourne, Australia

Merwin M (1989) *Casuarina cunninghamiana* - The River She-Oak. NFTA 89-06. Winrock International, Morrilton, Arkansas.

Midgley SJ (1990) The collection and distribution of *Casuarina* seed by the Australian Tree Seed Centre. Advances in Casuarina research and utilization. Proceedings of the Second International Casuarina Workshop, Cairo, Egypt, pp. 55-68

Morris TL, Esler KJ, Barger NN, Jacobs SM, Cramer MD (2011) Ecophysiological traits associated with the competitive ability of invasive Australian acacias. Divers Distrib 17:898–910

Morton JF (1980) The Australian pine or beefwood (*Casuarina equisetifolia* L.) an invasive ‘‘weed’’ tree in Florida. Proc Florida State Hort Soc 93:87–95

Muenier H (1990) Notes on *Casuarina equisetifolia* in Rodrigues. In: Advances in casuarina research and utilization. Proceedings of the Second International Casuarina Workshop, Cairo, Egypt, pp 233-234

Ndoye AL, Sadio O, Diouf D (2011) Genetic variation of *Casuarina equisetifolia* subsp *equisetifolia* and *C. equisetifolia* subsp *incana* populations on the northern coast of Senegal. Genet Mol Res 10:36-46

Nel JL, Richardson DM, Rouget M, Mgidi TN, Mdzeke N, Le Maitre DC, van Wilgen BW, Schonegevel L, Henderson L, Neser S (2004) A proposed classification of invasive alien plant species in South Africa: towards prioritizing species and areas for management action. S Afr J Sci 100: 53-64

NSW Government: Environment & Heritage (2012) Swamp She-oak – profile. http://www.environment.nsw.gov.au/threatenedSpeciesApp/profile.aspx?id=10152. Accessed 12 December 2012

Office of Technology Assessment (1993) Harmful non-indigenous species in the United States, OTA-f-565 – United States Government Printing Office

Ogunwande IA, Flamini G, Adefuye AE, Lawal NO, Moradeyo SO, Avoseh NO (2011) Chemical compositions of *Casuarina equisetifolia* L., *Eucalyptus toreliana* L. and *Ficus elastica* Roxb. ex Hornem cultivated in Nigeria. S Afr J Bot 77:645-649

Orians GH, Milewski AV (2007) Ecology of Australia: the effects of nutrient-poor soils and intense fires. Biol Rev 82:393–423

Orwa C, Mutua A, Kindt R, Jamnadass R, Anthony S (2009) Agroforestree Database: a tree reference and selection guide version 4.0. http://www.worldagroforestry.org/af/treedb/. Accessed 10 June 2012

Osundina MA (1997) Nodulation and growth of mycorrhizal *Casuarina equisetifolia* J.R and G. First in response to flooding. Bio Fertil Soils 26:95-99

Parrotta JA (1993) *Casuarina equisetifolia* L. ex J. R. & G. Forst. *Casuarina*, Australian pine. Research notes, New Orleans: USDA Forest Service, Southern Forest Experiment Station, pp 11-14

Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr 34:102–117

Pemberton RW (1996) The potential of biological control for the suppression of invasive weeds of southern environments. Castanea 61:313-319

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

Porter SS, Stanton ML, Rice KJ (2011) Mutualism and adaptive divergence: Co-invasion of a heterogeneous grassland by an exotic legume-Rhizobium symbiosis. PLoSONE 6(12): e27935. doi:10.1371/journal.pone.0027935

Poynton RJ (1995) Report to the Southern African Regional Commission for the Conservation and Utilization of the Soil (SARCCUS) on tree planting in southern Africa. Vol. 1. Other Genera - *Casuarina*. Department of Forestry, Pretoria, South Africa

Procheş Ş (2006) Latitudinal and longitudinal barriers in global biogeography. Biol Letters 2:69–72

Procheş Ş, Wilson JRU, Richardson DM, Rejmánek M (2012) Native and naturalized range size in *Pinus*: relative importance of biogeography, introduction effort and species traits. Global Ecol Biogeogr 21:513–523

Pyšek P, Křivánek M, Jarošík V (2009a) Planting intensity, residence time, and species traits determine invasion success of alien woody species. Ecol 90:2734–2744

Pyšek P, Jarošík V et al (2009b) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. Divers Distrib 15:891–903

Pyšek P, Richardson DM (2010) Invasive species, environmental change and management, and ecosystem health. Ann Rev Environ Res 35:25–55

Pyšek P, Richardson DM, Rejmánek M, Webster G, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53:131–143

Rejmánek M, Richardson DM (1996) What attributes make some species more invasive? Ecology 77:1655-1661

Rejmánek M, Richardson DM (2011) Eucalypts. In: Simberloff D, Rejmánek M (eds) Encyclopedia of biological invasions. University of California Press, Berkeley, pp 203–209

Rejmánek M, Richardson DM (2013) Trees and shrubs as invasive alien species – 2013 update of the global database. Divers Distrib 19: 1093-1094 doi: 10.1111/ddi.12075

Rejmánek M, Richardson DM, Higgins SI, Pitcairn MJ, Grotkopp E (2005) Ecology of invasive plants: state of the art. In Mooney HA, McNeely JA, Neville L, Schei PJ, Waage J (eds) Invasive alien species: searching for solutions. Island Press, Washington, D.C., pp 104-161

Ricciardi A (2006) Are modern biological invasions an unprecedented form of global change? Conserv Biol 21:329-336

Richardson DM (1989) Weeds and wealth. Conserva 4(3):7-9

Richardson DM (1998) Forestry trees as invasive aliens. Conserv Biol 12:18-26

Richardson DM (2006) *Pinus*: a model group for unlocking the secrets of alien plant invasions? Preslia 78:375–388

Richardson DM (ed) (2011) Fifty years of invasion ecology. The legacy of Charles Elton. Wiley-Blackwell, Oxford

Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M (2000) Plant invasions - the role of mutualisms. Biol Rev 75:65-93

Richardson DM, Benggeli P, Scroth G (2004) Invasive agroforestry trees: problems and solutions. In: Schroth G, de Fonseca GAB, Harvey CA, Gascon C, Vasconcelos HL, Izac A-MN (eds) Agroforestry and Biodiversity Conservation in Tropical Landscapes, Island Press, Washington, D.C., pp 371-396

Richardson DM, Bond WJ (1991) Determinants of plant-distribution – evidence from pine invasions. Am Nat 137:639–68

Richardson DM, Carruthers J, Hui C, Impson FAC, Miller JT, Robertson MP, Rouget M, Le Roux JJ, Wilson JRU (2011) Human-mediated introductions of Australian acacias – a global experiment in biogeography. Divers Distrib 17:771–787

Richardson DM, Pyšek P (2012) Naturalization of introduced plants: Ecological drivers of biogeographic patterns. New Phytol 196:383–396

Richardson DM, Rejmánek M (2004) Invasive conifers: A global survey and predictive framework. Divers Distrib 10:321-331

Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive alien species – a global review. Divers Distrib 17:788–809

Richardson DM, van Wilgen BW, Nunez M (2008) Alien conifer invasions in South America – short fuse burning? Biol Invas 10:573–577

Richardson DM, Williams PA, Hobbs RJ (1994) Pine invasions in the southern hemisphere: determinants of spread and invadability. J Biogeogr 21:511-527

Rockwood DL, Geary TF (1991) Growth of 19 exotic and two native tree species on organic soils in southern Florida. In: Proc. Symposium on Exotic Pest Plants, USDI National Park Service Report 1988, Miami, pp 283-302

Rogers J, Gamble D (2008) The impact of Hurricane Frances (2004) on the invasive Australian pine (*Casuarina equisetifolia*) on San Salvador Island, The Bahamas. J Torrey Botl Soc 135:367-376

Sandlund OT, Schei PJ, Viken Å (2001) Invasive species and biodiversity management. Dordrecht, Kluwer Academic Publishers

Sands DPA, New TR (2002) The Action Plan for Australian Butterflies. Environment Australia, Canberra

Savourie A, Lim G (1991) Characterization of an effective *Frankia* (ISU 0224887) isolated from nodules of *Gymnostoma sumatranum*. Plant Soil 131:21-27

Sayeed M, Siddiqui ZA (2008) AMF as potential bioprotectants against plant pathogens. Mycorrhizae: Sustain Agric For 61-97

Schlaepfer DR, Glättli M, Fischer M, Van Kleunen M (2010) A multi-species experiment in their native range indicates pre-adaptation of invasive alien plant species. New Phytol 185:1087–1099

Sealey N (2006) The cycle of *Casuarina*-induced beach erosion—a case study from Andros, Bahamas. In: Davis RL, Gamble DW (eds) The 12th Symposium on the Geology of the Bahamas and Other Carbonate Regions (2004). San Salvador, Bahamas: Gerace Research Center

Simberloff D, Nuñez M, Ledgard NJ, Pauchard A, Richardson DM, Sarasola M, van Wilgen BW, Zalba SM, Zenni RD, Bustamante R, Peña E, Ziller SR (2010) Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. Austral Ecol 35:489–504

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1:21–32

Smith CW (1998) Pest Plants of Hawaiian Native Ecosystems. University of Hawaii, USA: Department of Botany. http://www.botany.hawaii.edu/faculty/cw_smith/aliens.htm. Accessed 27 May 2012

Smith SE, Read DJ (2008) Mycorrhizal Symbiosis, third ed. Academic Press, San Diego

Snyder SA (1992) Casuarina spp. In: Fire Effects Information System. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). http://www.fs.fed.us/database/feis/. Accessed 9 April 2012

Steane DA, Wilson KL, Hill RS (2003) Using *mat*K sequence data to unravel the phylogeny of Casuarinaceae. Mol Phylogenet Evol 28(1):47-59

Strasberg D (1996) Diversity, size composition and spatial aggregation among trees on a 1-ha rain forest plot at La Réunion. Biodivers Conserv 5:825-840

Strauss SH, Ledig FT (1985) Seedling architecture and life history evolution in pines. Am Nat 125:702-715

Subramanean J, Reddy MV (2010) Effect of casuarina (*Casuarina equisetifolia*) plantation on the sand skink (*Eutropis bibronii* Gray 1839) population. Curr Sci 98(5):604-605

Swearingen JM (1997) Australian Pine. Washington, D.C. National Park Service, Plant Conservation Alliance, Alien Plant Working Group. http://www.nps.gov/plants/alien/fact/caeq1.htm. Accessed 14 May 2012

Tassin J, Lavergne C, Muller S, Blanfort V, Baret S, Le Bourgeois T, Triolo J, Rivière J-N (2006b) Bilan des connaissances sur les conséquences écologiques des invasions de plantes a l'île de la Réunion (Archipel des Mascareignes, Océan Indien). Rev Ecol (Terre Vie) 61:35-52

Tassin J, Rivière J-N, Cazanove M, Bruzzese E (2006a) Ranking of invasive woody plant species for management on Réunion Island. Weed Res 46:388–403

Taylor GS, Austin AD, Jennings JT, Purcell MF, Wheeler GS (2010) *Casuarinicola*, a new genus of jumping plant lice (Hemiptera: Triozidae) from *Casuarina* (Casuarinaceae). Zootaxa 2601:1–27

The Plant List (2010) A working list of all plant species. http://www.theplantlist.org/tpl/search?q=casuarina. Accessed 22 May 2012

Torrey JG, Berg H (1988) Some morphological features for generic characterization among the Casuarinaceae. Am J Bot 75:864-874

U.S. National Research Council (1984) Casuarinas: Nitrogen-fixing trees for adverse sites. National Academy Press, Washington D.C.

van Kleunen M, Schlaepfer DR, Glaettli M, Fischer M (2011) Pre-adapted for invasiveness: do species traits or their plastic responses to shading differ between invasive and non-invasive plant species in their native range? J Biogeogr 38:1294-1304

Varma A (2008) Mycorrhiza: genetics and molecular biology, eco-function, biotechnology, eco-physiology, structure and systematics. New York: Springer

Vergara NT, Nair PKR (1985) Agroforestry in the south pacific region - an overview. Agroforest Syst 3:363-379

Victorian Resources Online (2011) Belah. http://vro.dpi.vic.gov.au/dpi/vro/vrosite.nsf/pages/water_sss_belah. Accessed 12 December 2012

Vitousek PM (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7-13

Vitousek PM, Walker LR (1989) Biological invasion by *Myrica faya* in Hawaii: Plant demography, nitrogen fixation, ecosystem effects. Ecol Monogr 59:247–265

Wang B, Qiu YL (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16:299-363

Weber E (2003) Invasive plants of the World. CABI Publishing, Wallingford

Wheeler GS, Taylor GS, Gaskin JF, Purcell MF (2011) Ecology and management of Sheoak (*Casuarina* spp.), an invader of coastal Florida, USA. J Coastal Res 27:485-492

Whistler WA, Elevitch CR (2006) *Casuarina equisetifolia* (beach she-oak) *C. cunninghamiana* (river she-oak). Species profiles for Pacific Island

agroforestry. http://www.agroforestry.net/tti/Casuarina-she-oak.pdf. Accessed 12 June 2012

Williamson SL, Smith JE (2007) A greview of the distribution, taxonomy, and impacts of introduced seaweeds. Annu Rev Ecol Evol Syst 38:327–359

Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. Trends Ecol Evol 24:136–144

Wilson JRU, Gairifo C, Gibson MR et al (2011) Risk assessment, eradication, and biological control: global efforts to limit Australian acacia invasions. Divers Distrib 17:1030–1046

Wilson JRU, Richardson DM, Rouget M, Procheş Ş, Amis MA, Henderson L, Thuiller W (2007) Residence time and potential range: crucial considerations in modelling plant invasions. Divers Distrib 13:11-22

Wilson KL (1997) Casuarinaceae R. Brown: She-oak or *Casuarina* Family. In: Flora of North America Editorial Committee (ed.), Flora of North America, North of Mexico, volume 3, Oxford University Press, New York

Wilson KL, Johnson LAS (1989) Casuarinaceae. Flora of Australia. Volume 3 Hamamelidales to Casuarinales edition. Australian Government Publishing Services, Canberra

World Checklists for Selected Plant Families (WCSP) (2010) The Board of Trustees of the Royal Botanic Gardens. www.kew.org/wcsp/. Accessed 20 February 2012

Worldclim (2005) Worldclim database, version 1.4 (release 3). Berkeley, CA Museum of Vertebrate Zoology, University of California, Berkeley. http://www.worldclim.com. Accessed 25 February 2012

Zhong C (1993) Study on the optimum *Frankia*-genotype associations of *Casuarina* seedlings. Forest Res 6:654-660

Zhong C, Gong M, Chen Y, Wang F (1995) Inoculation of *Casuarina* with mycorrhizal fungi and *Frankia*. In: Brundrett M, Dell B, Malajczuk N, Gong M (eds) Mycorrhizas for

Plantation Forests in Asia. ACIAR Proceedings No.62, CSIRO, Canberra, pp 122-126

Zhong C, Zhang Y, Chen Y, Chen Z, Jiang Q, Pinyopusarerk K, Franche C (2010a) Potential Casuarina species and suitable technology for the GGW. In: Dia A, Duponnois R, Wade A (eds) The major project of the African Great Green Wall: Concepts and implementation. IRD, Marseille, pp 163-170

Zhong C, Zhang Y, Chen Y, Jiang Q, Chen Z, Liang J, Pinyopusarerk K, Franche C, Bogusz D (2010b) *Casuarina* research and applications in China. Symbiosis 50:107–114

Zhongze Z, Torrey JG (1985) Studies of an effective strain *of Frankia* from *Allocasuarina lehmanniana* of the Casuarinaceae. Plant Soil 87:1-16

Box 2.1: *Casuarina* in Florida, USA

This case study provides useful insights on the rationale behind introductions of *Casuarina* species, their impacts, changing views of the benefits and costs of casuarinas, and the evolution of management strategies.

Introduction history and uses

Seeds of four *Casuarina* species (*C. cristata*, *C. cunninghamiana*, *C. equisetifolia* and *C. glauca*) were introduced to the USA from France in 1898. These species were planted along beaches and near homes for protection against hurricanes and strong winds (Schmid et al. 2008). Seeds were often distributed under erroneous names and misidentification is still a problem (Morton 1980). *Casuarinas* were initially used for forestry, but the arrival of bacterial canker (spread by wind-blown rain) on citrus in 1995 led to an increase in their use as windbreaks (Fig. 1f). *Casuarina cunninghamiana* was most widely used for this purpose based on its successful use for this purpose elsewhere in the world and its apparent non-invasiveness (Castle et al. 2008).

Impacts

Casuarina cunninghamiana, *C. equisetifolia* and *C. glauca* and are currently considered among the most severe invaders in Florida (Wheeler et al. 2011). These three species and their hybrids aggressively invade inland (Fig. 2a and f) and coastal habitats and threaten biodiversity and beach integrity (Morton 1980). *Casuarina equisetifolia* and *C. glauca* have transformed beach, dune, and coastal scrub communities into closed-canopy forests with little understorey (Gordon 1998). *Casuarina equisetifolia* has had a range of effects in invaded ecosystems, including increased erosion rates resulting from exclusion of native soil stabilizers (Crooks 2002). This species out-competes native plants and replaces entire natural plant communities (Brock et al. 1997). High rates of litterfall from *C. equisetifolia* can potentially suppress the recruitment of other species (Gordon 1998). Nesting of loggerhead sea turtles is physically impeded by fallen trees and the formation of steep shorelines (Office of Technology Assessment 1993). Rodent densities and understorey growth are reduced (Crooks 2002). Casuarinas also pose a threat to human health as the seasonal release of pollen results in respiratory ailments (Morton 1980). During hurricanes the fallen branches and/or trees (up to 30m) directly damage homes, power lines, power poles, and block evacuation roads. In northern areas of the state, frost-killed trees become problematic due to the fall of branches and crowns (McNeely et al. 2011).

Management

The Florida Exotic Pest Plant Council (FLEPPC) (2003) defined these three species as ‘‘invasive exotics that are altering native plant communities by displacing native species, changing community structures or ecological functions, or hybridizing with natives”. *Casuarina equisetifolia* and *C. glauca* are classified as Category 1 invaders, and *C. cunninghamiana* as a Category 2 invader (FLEPPC Plant List Committee 2003). They are prohibited under state environmental policies and cannot be held, collected, transported, cultivated, or imported without a permit from the Department of Agriculture and Consumer Services. This Department is currently developing and implementing a monitoring protocol to determine the invasiveness of *C. cunninghamiana*.

A hurricane in 1986 caused extensive damage due to wind-blown casuarinas on Sanibel Island off Florida coast and triggered management action. Efforts to remove all casuarinas from this area (state-owned and private land) and re-vegetate with native plants are underway.

No specific management plans are being implemented for casuarinas elsewhere in Florida, but guidelines have been proposed for their control (Langeland et al. 2011). Recommended herbicide treatments are: Basal bark application: 10% - 20% Garlon 4; Cut stump: 50% Garlon 3A or 10% - 20% Garlon 4 (remove scaly bark if present); Frill (larger trees): 20% Garlon 4. The addition of 3% Stalker will increase consistency on older trees; Soil: 4-6 pounds Velpar ULW/acre.

The Australian Biological Control Laboratory in Brisbane, Australia, in collaboration with the US Department of Agriculture, are investigating host range and host specificity of potential insect herbivores for the biological control of casuarinas (CSIRO 2011). A number of insects have been identified as potential agents. Priority is being given to foliage- and seed-feeding insects such as gall-forming wasps, defoliating moths and seed feeders (CSIRO 2011). Genetic studies are being conducted to determine the variation in *Casuarina* species in Australia and Florida to locate the source populations of the weed in the introduced range (CSIRO 2011). Research into the evolutionary associations between *Casuarina* and its associated herbivores is also planned (CSIRO 2011).

Box 2.2: *Casuarina* in the Mascarene Islands

Casuarinas are now emblematic of the Mascarene Islands, an archipelago in the southern Indian Ocean east of Madagascar comprising Mauritius, La Réunion and Rodrigues. Many shops, hotels, restaurants are named 'filao' - the local name for casuarinas. This case study provides insights into the varying levels of success achieved by casuarinas, and reveals how different perceptions *and management efforts have developed o*n different islands.

La Réunion Island

The native flora of Réunion Island is threatened by many invasive woody plants introduced for agriculture, forestry or as ornamentals (Tassin et al. 2006a). Among these are *Casuarina cunninghamiana* (introduced in 1840), *C. glauca* (introduced in 1877), and *C. equisetifolia* (introduced in 1768) (Baret et al. 2006). These species were mainly used for firewood, but also for erosion control (Kueffer and Vos 2004). By the early 1900s, all fuel-wood used in the lowlands came from *Casuarina* plantations around the coast (Cheke and Hume 2008). By the 1920s, over a million *Casuarina* trees had been planted on the island (Cheke and Hume 2008). After World War II, the Forest Service began large-scale planting to replace natural forest with alien trees, mainly species of species of *Acacia*, *Casuarina* and *Cryptomeria* (Kueffer and Lavergne 2004). Low-altitude habitats were greatly reduced, transformed and fragmented by the combination of human activities (agriculture, urbanization) and invasion by introduced species (Strasberg 1996). Currently, large-scale disturbances such as lava flows, fire and hurricanes may facilitate *C. equisetifolia* invasions on the island. *Casuarina equisetifolia* has increased substantially in abundance and distribution since Macdonald et al.'s (1991) ranking of invasive plant species (Baret et al. 2006). *Casuarina cunninghamiana* invades inland slopes at higher altitudes (Baret et al. 2006) while *C. glauca*, which is not mentioned by Macdonald et al. (1991), also invades upland areas of the island (Tassin et al. 2006b).

Impacts

Casuarina equisetifolia is a major transformer species on La Réunion and invades volcanic lava flows (Fig. 2d) and coastal regions where it forms dense monospecific stands, affects nutrient cycling (Kueffer and Lavergne 2004), and interferes with early natural succession (Macdonald et al. 1991). The impacts of *C. cunninghamiana* and *C. glauca* on the island have not yet been assessed.

Management

In 2007 the forestry service initiated a control programme for *C. equisetifolia* along the south-eastern coast (supralittoral zone) with the aim of restoring coastal habitat. At local scales, results have been promising, and native species have started to re-emerged. No management attempts have been made for *C. cunninghamiana* and *C. glauca.* The forestry sector is currently shifting emphasis from production forestry to nature conservation and invasive species control. A national invasive species committee has been set up and on-going research projects attempt to assess the impacts of control methods. Problem species and areas have been prioritised for control. Options for biological control of casuarinas have not yet been assessed.

Mauritius

Increased agriculture, the emancipation of slaves, the demand for wood for the railways, and the introduction of alien plant species during the 18th century contributed to the degradation of the native forest (Kueffer and Mauremootoo 2004). The first seedlings of *C. equisetifolia* were brought to the island in 1778, and British colonialists distributed seedlings all over the island (Cheke and Hume 2008). Large-scale reforestation started in the late 19th century and continued until the mid-1970s (Kueffer and Mauremootoo 2004). Casuarinas were planted along the coastline as part of a tree and water conservation programme and to protect against beach erosion and sea gusts (Cheke and Hume 2008). *Casuarina equisetifolia* is now naturalized (Sandlund et al. 2001) and has begun to spread in certain areas - e.g. on Ile aux Benitiers, off the southwest coast where plantations have reached maturity and regenerate spontaneously and on Le Morne Mt. where individuals are spreading up the mountain flank from a plantation (Cheke and Hume 2008). A plantation of another *Casuarina* species (yet to be identified) has been established inland near the Cabinet Nature Reserve, but no spread has been observed (Cheke and Hume 2008).

Impacts

Impacts for casuarinas on Mauritius have yet to be assessed.

Management

The island is still in the phase of planting *C. equisetifolia* rather than controlling it. There have, however, been recommendations to remove the species from coastal areas and to replace it with a more native tree mix for shade and erosion control.

Rodrigues Island

The human population on this small island (109 km²) grew from 100 to 35 000 between 1800 and 1950. In 1845, most of the natural forest had been removed through tree felling, wood burning, browsing (by goats), trampling (by cattle), rooting (by pigs), and overgrazing. It was then suggested that the island could support more than 12000 cattle if a "few improvements" were done (Cheke and Hume 2008). Among these "improvements" was the planting of *C. equisetifolia* in the uplands; the species was introduced in 1876. In the early 1900s, the planting of casuarinas was again recommended in coastal areas and on light soils provide shade and improve grass cover. "Agricultural improvements" commenced again in 1955, when large areas of natural forest were cut and replanted with alien trees such as casuarinas for timber production and watershed protection (Cheke and Hume 2008). While casuarinas produced firewood, they did not provide food or shelter to endemic wildlife or supply sufficient shade for effective cover on dry slopes. They are used for hedges, fences, windbreaks, fuel-wood, and timber for fishing boats and house construction (Muenier 1990). *Casuarina equisetifolia* is now naturalized (Sandlund et al. 2001).

Impacts

The impacts of *C. equisetifolia* on Rodrigues Island have yet to be assessed.

Management

A pilot coastal restoration project funded by European Union from 2002-2003 was implemented to restore native vegetation in two contrasting coastal plots (areas planted with *C. equisetifolia*). This project aims to establish workable methodologies for future coastal restoration through experimentation.

Tables

Table 2.1 *Casuarina* taxonomy as used in this paper (derived from The Plant List 2010)

	***Casuarina* species**
1	*C. collina* Poiss. ex Pancher and Sebert
2	*C. cristata* Miq.
	C. cristata subsp. *cristata**
	C. cristata subsp. *pauper**
3	*C. cunninghamiana* Miq.
	C. cunninghamiana subsp. *cunninghamiana*
	C. cunninghamiana subsp. *miodon*
4	*C. equisetifolia* L.
	C. equisetifolia subsp. *incana* (Benth.) L.A.S. Johnson
	C. equisetifolia subsp. *equisetifolia*
5	*C. glauca* Sieber ex Spreng.
6	*C. grandis* L.A.S. Johnson
7	*C. junghuhniana* Miq.
	C. junghuhniana subsp. *timorensis**
	C. junghuhniana subsp. *junghuhniana**
8	*C. obesa* Miq.
9	*C. oligodon* L.A.S. Johnson
	C. oligodon subsp. *abbreviata**
	C. oligodon subsp. *oligodon**
10	*C. orophila* L.A.S. Johnson
11	*C. pauper* F. Muell. ex L.A.S. Johnson

12	*C. potamophila* Schltr.
13	*C. tenella* Schltr.
14	*C. teres* Schltr.

* Taxa which have an unresolved taxonomy as listed by the World Checklists for Selected Plant Families (WCSP 2010).

Table 2.2 Naturalization and climate suitability are correlated. Contingency table of 97 instances where *C. cunninghamiana, C. equisetifolia* and/or *C. glauca* have been introduced to a country. Naturalization was recorded in 36 countries, only 4 of which were in climatically unsuitable areas (i.e. model errors). In another 61 cases, no naturalization is recorded. *Casuarina cunninghamiana, C. equisetifolia* and/or *C. glauca* have been introduced to 37 climatically suitable countries where they have not yet become naturalized (Table 2) – suggesting a substantial invasion debt. Climatic suitability was determined based on the model where the lowest presence threshold (Pearson et al. 2007) was used to define climatically suitable areas on a continuous scale of 0 to1 (0 = low suitability and 1 = high suitability). Naturalization (sensu Pyšek et al. 2004) in each country was determined by evidence in the literature. 'Y' = Yes and 'N' = No. Chi-square = 8.78; $p<0.05$

	Naturalized	
Climatically suitable	Y	N
Y	32 Correctly predicted naturalizations	37 Potential invasion debt
N	4 model errors	24 Plantations in areas unsuitable for naturalization

Table 2.3 Selected life-history traits and environmental preferences for *Casuarina* species

***Casuarina* species**	**Breeding System**	**Max. tree height (m)**	**Samara length (mm)**	**Seed size (mean number of seeds kg^{-1})**	**Coppicing ability**	**Propagation**	**Nodulation**	**Status as introduced taxa (sensu Pyšek et al. 2004)**	**Tolerance of abiotic factors**	**Factors potentially limiting naturalization/invasion**
C. collina	dioecious[5]	15-20[5]	?	?	?	root suckering[5], seed[5]	present[5]	alien	fire resistant[5], infertile soil[5]	?
C. cristata	dioecious[12]	10-20[2]	3-4[2]	111 900[11]	yes[2]	root suckering[12], seed[2]	minimal[2]	alien	drought[12], moderately saline soils[2], waterlogging[2], frost[2]	seedlings and suckers grazed by livestock[12]
C. cunninghamiana	dioecious[12]	12-35[11]	3-4[11]	607 200[11]	yes[11]	root suckering[12], seed[15]	prolific[12]	invasive	cold temperatures[12], drought, moderate soil salinity[15], frost[15],	seedlings susceptible to browsing[12], fire-sensitive[11]

									wind[15]	
C. equisetifolia	monoecious[1,2]	6-35[11]	4-5[15]	268 200[11]	yes[12]	seed and/or vegetative[15]	prolific[12]	invasive	infertile soil[12], drought[15], coastal salt spray[15], high soil salinity[15], waterlogging[15], wind[15]	browse-[12], fire-[12], frost-[12], and shade-sensitive[12], cold temperatures[12], seedlings susceptible to disease[12], susceptible to root rot[12]
C. glauca	dioecious[12]	8-20[11]	3.5-5[11]	414 900[11]	yes[12]	root suckering[12], seed[12]	prolific[12]	invasive	coastal salt spray[12], waterlogging [12], drought[12], highly saline, acidic and alkaline soil[12]	suckers grazed by livestock[12], frost-sensitive[12]
C. grandis	dioecious[8]	35-40[8]	?	?	?	root suckering[8],	present[13]	alien	?	?

						seed[8]				
C. junghuhniana	dioecious[12]	15-25[11]	4-5[11]	1000 000 – 1800 000[11]	yes[12]	root suckering[12], seed and/or vegetative[16]	minimal[12]	alien	drought[12], waterlogging[11]	hybrid trees do not produce seeds[7,12]
C. obesa	dioecious[12]	3-15[10]	5-7[10]	840 000[12]	no[4]	root suckering[12], seed[1]	prolific[12]	alien	drought[4], high soil salinity[10], waterlogging[10], frost[10], wind[10]	suckers grazed by livestock[4]
C. oligodon	dioecious[12]	30[11]	4[11]	1500 000 – 2000 000[11]	yes[11]	seed[11], epicormic shoots[12]	present[12]	alien	high humidity[12]	sensitive to saline soils[12], susceptible to wind damage[12]
C. orophila	?	?	?	?	?	?	present[13]	?	?	?
C. pauper	dioecious[14]	6-15[14]	?	?	?	seed[14]	?	?	moderate soil salinity[14], waterlogging[14]	?

C. potamophila	?	?	?	?	?	?	?	?	?	?
C. tenella	?	?	?	?	?	?	?	?	?	?
C. teres	?	?	?	?	?	?	?	?	?	?

[1]Blake (2009); [2]Turnbull (1997); [3]Elfers (1988); [4]*Emmott and Greening Western Australia (2001);* [5]Gauthier et al. (1999); [6]Halliday (1984); [7]Jayaraj (2010); [8]Johnson (1982); [9]Marcar and Crawford (1995); [10]NSW Government (1995); [11]Orwa et al. (2009); [12]U.S. National Research Council (1984); [13]Varma (2008); [14]Victorian Resources Online (2011); [15]Whistler and Elevitch (2006); [16]Zhong et al. (2010a)

Figures

Fig 2.1 Examples of uses for *Casuarina* species around the world. (a) The mining company Richards Bay Minerals (RBM) uses *C. equisetifolia* as part of their rehabilitation programme in KwaZulu-Natal, South Africa (photograph: LJ Potgieter). (b) *C. equisetifolia* planted along the beach of Cape Vidal, KwaZulu-Natal, South Africa, for dune stabilisation and shade (photograph: LJ Potgieter). (c) *C. equisetifolia* used for ornament in KwaZulu-Natal, South Africa (photograph: LJ Potgieter). (d) *C. equisetifolia* used for charcoal production at RBM, South Africa (photograph: LJ Potgieter). (e) *C. equisetifolia* planted for drift-sand reclamation on the beach of St. Lucia, KwaZulu-Natal, South Africa (photograph: LJ Potgieter). (f) *C. cunninghamiana* planted as a windbreak in Florida, USA (photograph: GS Wheeler). (g) *C. oligodon* planted with coffee in Mount Hagen, Papua New Guinea (photograph: S Midgley). (h) *C. equisetifolia* used as poles in Tamil Nadu, India (photograph: T Maari). (i) *C. equisetifolia* plantation used as a barrier from salt spray, pollution and wind in Batticaloa, Sri Lanka (photograph: Science Navigators). (j) *C. equisetifolia* cultivated for pulp and paper in Andhra Pradesh, India (photograph: JK Jain). (k) Locals harvesting *C. equisetifolia* in Andrha Prades, India (photograph: S Midgley). (l) Use of *Casuarina* in construction (photograph: P Visser)

Fig. 2.2 Examples of landscapes invaded by *Casuarina* species in different parts of the world. (a) *C. equisetifolia* invading along a road in Florida, USA (photograph: GS Wheeler). (b) Dense stands of self-sown *C. glauca* spreading in Hanaula (Maui), Hawaii (photograph: F and K Starr). (c) *C. glauca* invading Kapapa, Oahu, Hawaii (photograph: F and K Starr - fstarr@hawaii.rr.com). (d) Spectacular invasion of *C. equisetifolia* on lava flows, La Réunion Island, southern Indian Ocean (photograph: LJ Potgieter). (e) *C. equisetifolia* saplings invading the coastline of Mbudya Island, Tanzania (photograph: A Witt). (f) Dense stand of *C. equisetifolia* saplings in Florida, USA (photograph: GS Wheeler). (g) *C. equisetifolia* invading Hana (Maui), Hawaii (photograph: F and K Starr). (h) *C. equisetifolia* invading the Cayman Islands (photograph: C Clubbe). (i) *C. equisetifolia* invading the St. Lucia estuary in KwaZulu-Natal, South Africa (photograph: LJ Potgieter)

Fig. 2.3 Diversity of (a) native and (b) introduced (c) naturalized and (d) predicted *Casuarina* species world-wide at a 15^0 scale. Data from Australia's Virtual Herbarium, Global Biodiversity Information Facility, Atlas of Living Australia and Invasive Species Compendium

Fig. 2.4 The number of countries in which *Casuarina* species were first introduced during the respective time frame. Note that the last time frame is only 12 years. Most documented introductions of casuarinas occurred during the second half of the 20th century. Data from the Australian Tree Seed Centre

Fig. 2.5 The relationship between a) native and naturalized range sizes and b) number of references in the forestry literature and native range size in *Casuarina* species (number of 15° squares occupied; symbols jittered to show multiple species with identical values)

Figure 2.1

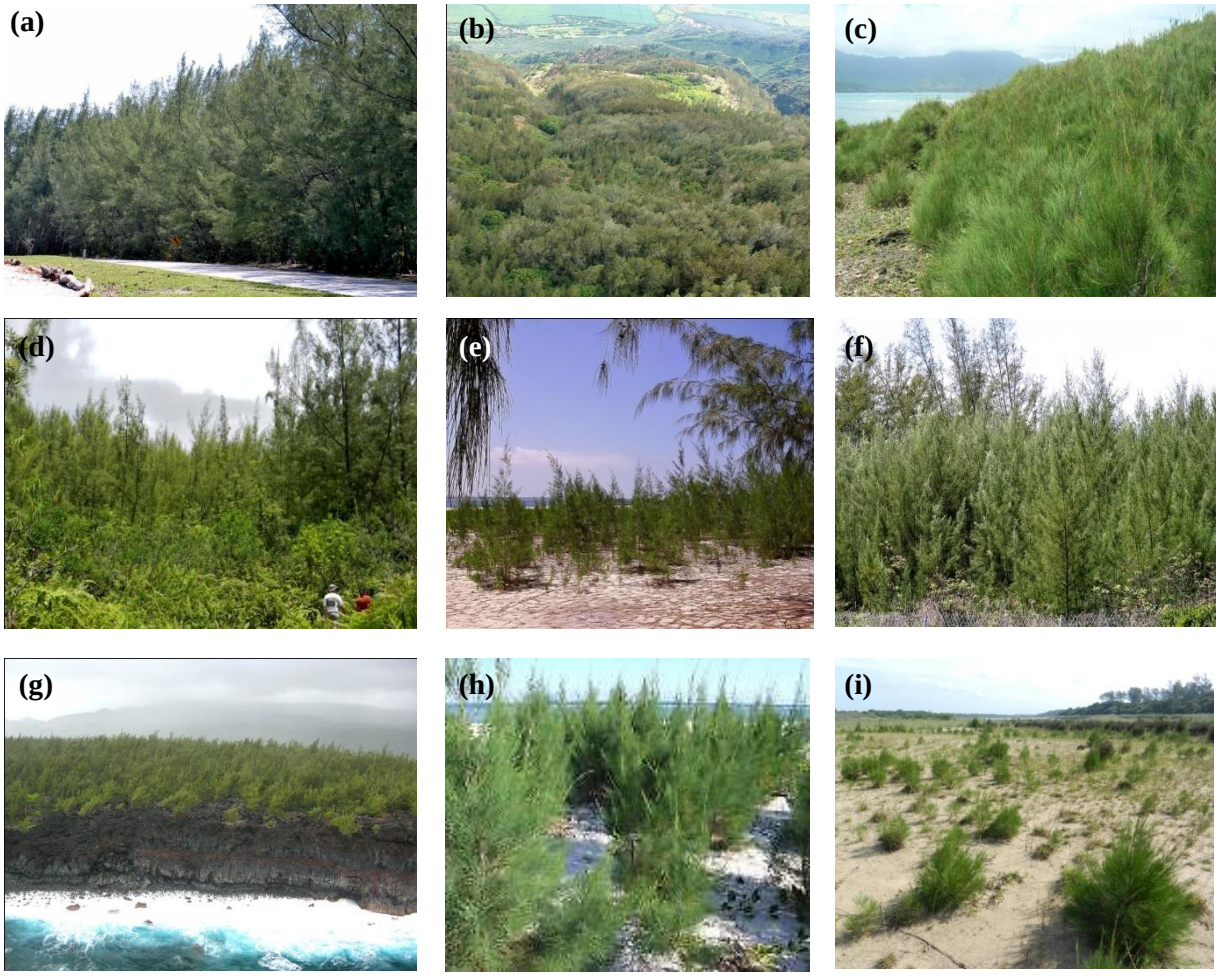

Figure 2.2

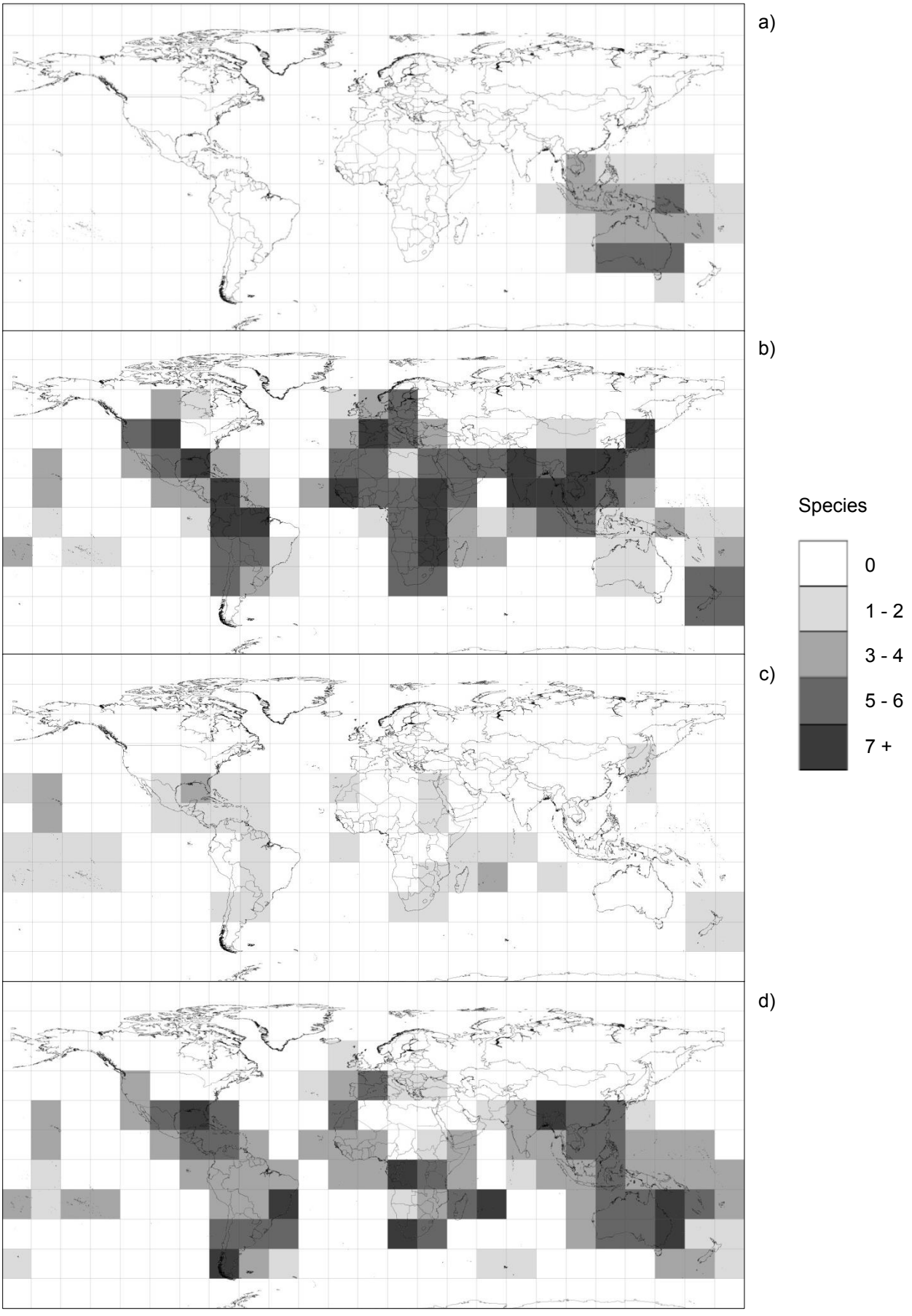

Figure 2.3

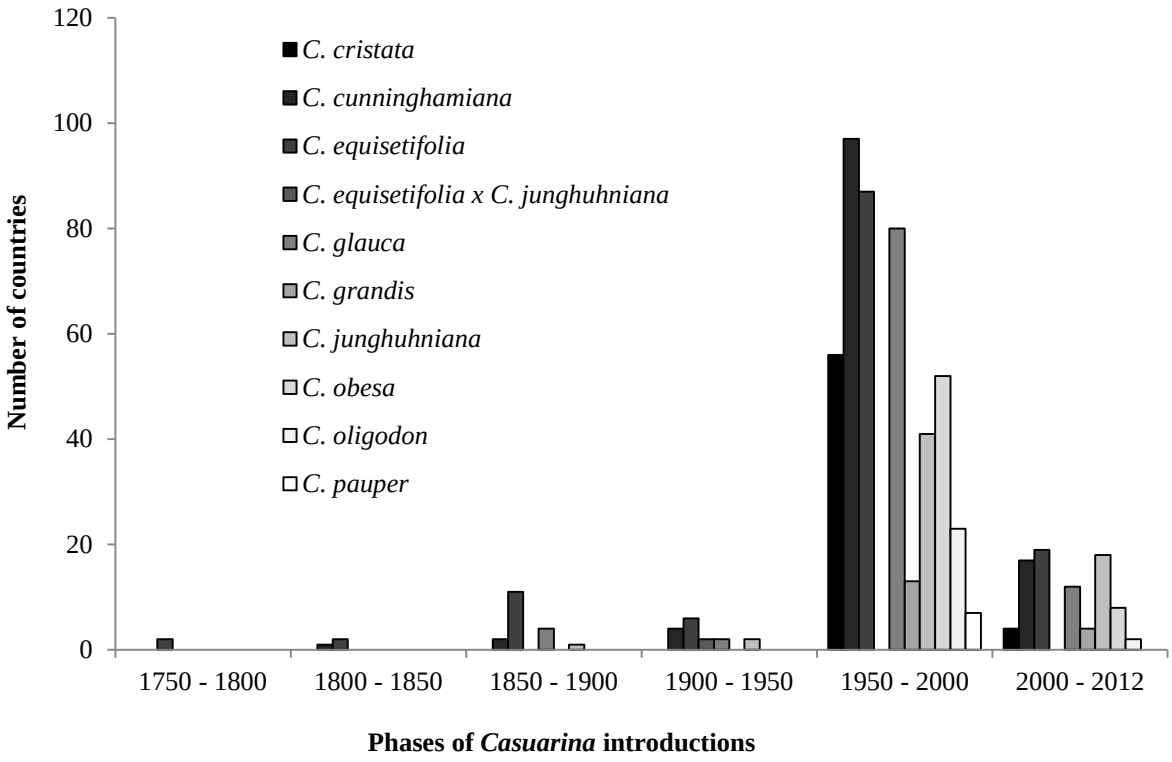

Figure 2.4

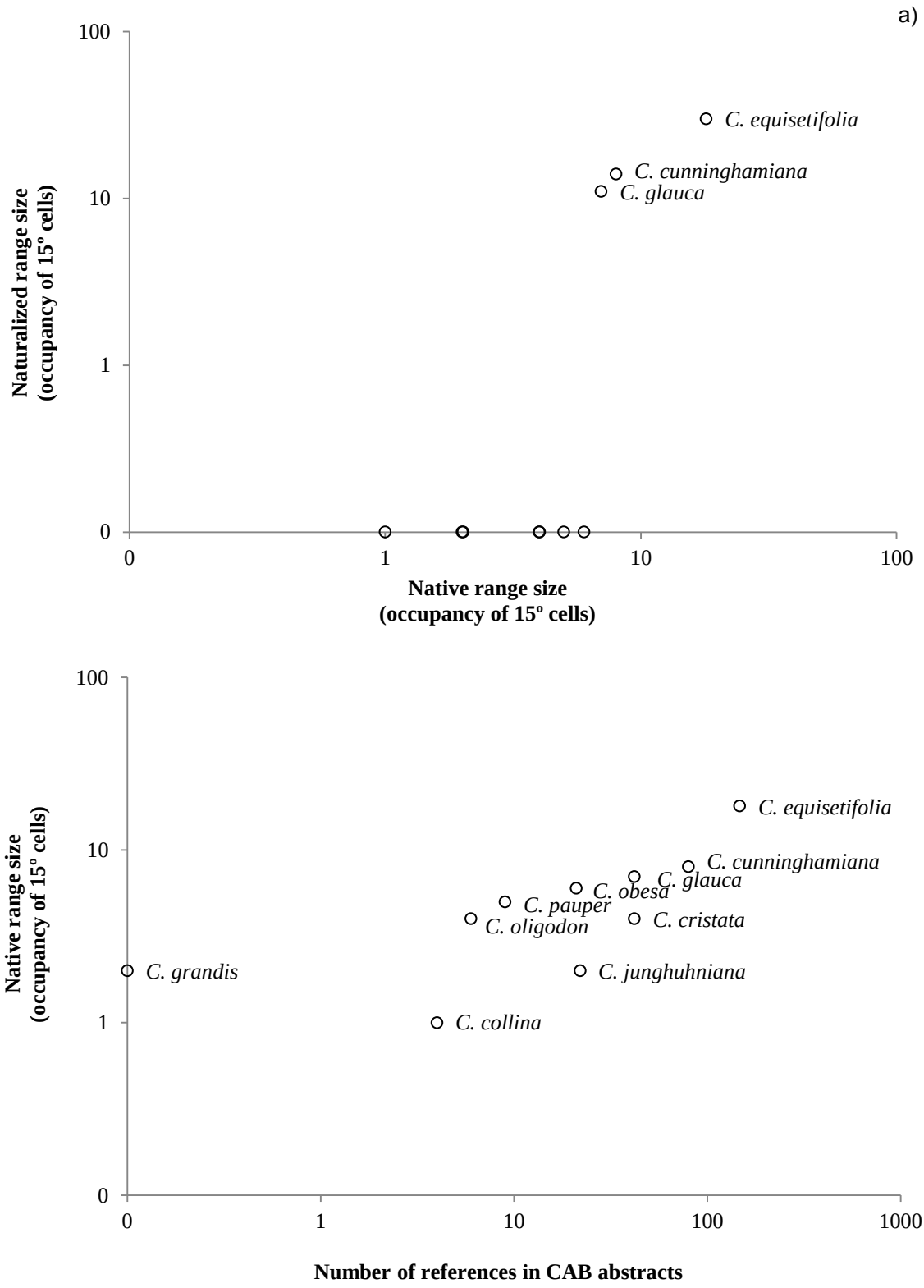

Figure 2.5

Supplementary Tables

Table S2.1 *Casuarina* introductions and large-scale cultivation around the world

Country	Species	Introduction Dates	Naturalisation	Large-scale Cultivation	Early Provenance Trials	Provenance of introductions
Africa (rest)						
Benin	C. equisetifolia	1992	N	700 ha		
Egypt	C. glauca	1977	N		1982, 9 provenances	Australia
	C. cunninghamiana	1977	N		1982, 18 provenances	Australia
	C. cristata	1982	N			
	C. equisetifolia	1970s	N	1970s - ±1 million seedlings sown 1980 - ±4 million seedlings sown	1992, 11 provenances	Australia, Egypt, Guam, India, Kenya, Malaysia, Papua New Guinea, Philippines, Vietnam
	C. obesa	1981	N			
Kenya*	C. equisetifolia	1900	N	1971 in Gede	1993, 25 provenances in Gede	Australia, China, Egypt, Fiji, Guam, India, Kenya, Malaysia, Benin, Philippines, Sri Lanka, Thailand, Vietnam, Vanuatu
	C. cristata	1981	N			
	C. cunninghamiana	1908	N			
	C. glauca	1910	N			
	C. grandis	1989	N			
	C. junghuhniana	1956	N			
	C. obesa	1983	N			
	C. oligodon	1990	N			
Morocco	C. cristata	1996	N			
	C. cunninghamiana		N			
	C. equisetifolia	1996	N			

	C. glauca		N			
	C. obesa	1996	N			
Niger	C. cristata	1982	N			
	C. equisetifolia		N			
	C. obesa	1984	N			
Nigeria	C. cunninghamiana	1989	N			
	C. equisetifolia		N			
	C. glauca	1991	N			
Senegal	C. cunninghamiana	1981	N			
	C. equisetifolia	1925	N	1948 ±126 000 ha in total	1940s in Niayes region	
	C. glauca	1995	N			
	C. junghuhniana	1984	N			
	C. obesa	1982	N			
	C. oligodon	1984	N			
	C. pauper	1984	N			
Sudan	C. equisetifolia	1985	N			
	C. cristata	1984	N			
	C. cunninghamiana	1984	Y			
	C. glauca	1985	N			
	C. obesa	1984	N			
Tunisia	C. cunninghamiana		N			
	C. glauca		N			
	C. obesa	1999	N			
Africa (Southern)						
Botswana	C. cristata	1986	N			
	C. cunninghamiana	1987	N	1980		
	C. equisetifolia	1983	N			
	C. glauca	1987	N			
	C. obesa	1986	N			

Mozambique	C. cristata	1984	N			
	C. cunninghamiana	1984	N			
	C. equisetifolia	1985	N	1400 ha		
	C. glauca	1988	N			
	C. junghuhniana	1999	N			
South Africa	C. cristata	1990s	N			
	C. cunninghamiana	1902 – 1907	Y*	1920s		
	C. equisetifolia	1858	Y	1950s		
	C. glauca	1898	N	1960s		
	C. junghuhniana	1994	N			
	C. obesa	1994	N			
	C. oligodon	1994	N			
Tanzania	C. cristata	1981	N			
	C. cunninghamiana	1981	N			
	C. equisetifolia	1983	N			
	C. glauca	1981	N			
	C. grandis	1988	N			
	C. junghuhniana	1990	N		1997, 28 provenances	Indonesia
	C. obesa	1986	N			
	C. oligodon	1993	N			
Zambia	C. cristata	1983	N			
	C. cunninghiama	1983	N			
	C. equisetifolia	1985	N			
	C. glauca	1985	N			
Zimbabwe	C. equisetifolia	1984	N			
	C. cristata	1984	N			
	C. cunninghamiana	1984	Y			
	C. glauca	1983	N			
	C. junghuhniana	1962	N			
	C. obesa	1984	N			
Asia						

India	C. cristata	1981	N		1916 Orissa State	
	C. cunninghamiana	1950	N			
	C. equisetifolia	1868	N	2005 Tamil Nadu – 4700 ha ±500 000 ha in total	1916 Orissa State 1979 Establishment of ITC Bhadrachalam Paperboards Ltd. In Andhra Pradesh 1990, 6 provenances on coast of Neyveli and Sadivayal	India, Australia, China, Thailand
	C. equisetifolia x C. junghuhniana	1951	N			
	C. glauca	1981	N			
	C. grandis	1990	N			
	C. junghuhniana	1984	N		1916 Orissa State	
	C. obesa	1985	N			
	C. oligodon	1982	N			
	C. pauper	1985	N			
Japan	C. cristata	1991	N			
	C. cunninghamiana	1982	N			
	C. equisetifolia	1988	Y*			
	C. glauca	1982	N			
	C. grandis	1991	N			
	C. junghuhniana	1991	N			
	C. obesa	1991	N			
	C. oligodon	1991	N			
Pakistan	C. cristata	1982	N			
	C. cunninghamiana	1981	N			
	C. equisetifolia	1983	N		1995, 16 provenances (25 plants each)	Australia, China, Egypt, Fiji, Guam, India, Kenya, Malaysia, Papua New Guinea, Philippines, Sri Lanka, Thailand, Vietnam, Vanuatu
	C. glauca	1982	N			

	C. junghuhniana	1996	N			
	C. obesa	1982	N			
People's Republic of China (PRC)	C. collina	1997	N			
	C. cristata	1983	N		1985 – 1991, 5 provenances	Australia
	C. cunninghamiana	1897	N		1986, 28 provenances	Australia, China
	C. equisetifolia	1897	N	1954 ±1.300 000 ha	1919 in Fujian province 1939 – 1945 in Guangdong 1950s in Guangxi and Zhejian province 1986, 12 provenances	Australia, China, Thailand
	C. glauca	1897	N		1986, 10 provenances	Australia, China
	C. grandis	1987	N		1985 – 1991, 1 provenance	Papua New Guinea
	C. junghuhniana	1897	N		1986, 8 provenances	Australia, Indonesia, Tanzania, Kenya
	C. obesa	1989	N		1985 – 1991, 2 provenances	Australia
	C. oligodon	1982				
Republic of China (ROC) (Taiwan)	C. cristata	1981	N			
	C. cunninghamiana	1981	N			
	C. equisetifolia	1897	N			
	C. glauca	1981	N			
	C. junghuhniana	1981	N			
	C. obesa	1993	N			
	C. oligodon	1981	N			
Sri Lanka	C. cristata	1984	N			
	C. cunninghamiana	1982	N			
	C. equisetifolia	1930s	N		1995, 15 provenances 3000 ha in total	Australia, China, Egypt, Guam, Malaysia, Papua New Guinea, Philippines, Solomon Islands, Thailand, Vietnam, Vanuatu
	C. glauca	1983	N			
	C. grandis	1988	N			
	C. junghuhniana	1984	N			
	C. obesa	1981	N			

	C. oligodon	1997	N			
Thailand	C. cristata	1984	N			
	C. cunninghamiana	1981	N			
	C. equisetifolia	1981	N			
	C. equisetifolia x C. junghuhniana	1900	N			
	C. glauca	1981	N			
	C. junghuhniana	1900	N		1992, 29 provenances in Ratchaburi and Chachoengsao	Australia, China, Egypt, Fiji, Guam, India, Kenya, Malaysia, Papua New Guinea, Philippines, Sri Lanka, Thailand, Vietnam
	C. obesa	1984	N			
	C. oligodon	1984	N			
Vietnam	C. cunninghamiana	1982	N			
	C. equisetifolia	1896	N	±120 000 ha	1915 coastal area of Nghe An 1929 north coast for mining poles	
	C. glauca	1982	N			
	C. junghuhniana	1985	N			
	C. oligodon	1995	N			
Atlantic Ocean Islands						
Bermuda	C. equisetifolia	1918	Y*			
Caribbean Region						
Bahamas	C. equisetifolia		Y*			
Barbados	C. equisetifolia	1870	Y*			
	C. obesa	1988	N			
Costa Rica	C. cristata	1983	N			
	C. cunninghamiana	1987	N			

	C. equisetifolia	1987	Y*			
	C. glauca	1983	N			
	C. junghuhniana	1997	N			
Cuba	C. cunninghamiana	1983				
	C. equisetifolia	1830	Y*			
Turks and Caicos Island	C. equisetifolia		Y*			
Central America						
Guatemala	cunninghamiana	1983	N			
Mexico	C. cristata	1982	N			
	C. cunninghamiana	1982	N			
	C. equisetifolia	1850s	Y			
	C. glauca	1984	N			
	C. grandis	2006	N			
	C. obesa	1988	N			
Nicaragua	C. cunninghamiana	1992	N			
	C. equisetifolia	1987	N			
Panama	C. cunninghamiana	1984	N			
	C. equisetifolia	1995	N			
Europe						
Spain	C. cunninghamiana		N			
	C. equisetifolia		N			
	C. glauca	2008	N			
	C. obesa	2008	N			
Indian Ocean Islands						
Madagascar	C. cunninghamiana	1983	N			

	C. equisetifolia	1996	Y*			
	C. glauca	1983	N			
Mauritius	C. equisetifolia	1778	Y*			
Réunion Island	C. cunninghamiana	1840	Y*			
	C. equisetifolia	1768	Y*			
	glauca	1877	Y*			
Rodriguez	C. equisetifolia		Y			
Indonesia						
Indonesia	C. cristata	1982	N			
	C. cunninghamiana	1982	N			
	C. equisetifolia	1984	N			
	C. glauca	1982	N			
	C. grandis	1987				
	C. junghuhniana	1990	N			
	C. oligodon	1982	N			
Middle East						
Israel	C. cristata	1981	N			
	C. cunninghamiana	1984	N			
	C. glauca	1981	N			
	C. obesa	1984	N			
Jordan	C. cristata	1991	N			
	C. equisetifolia		N			
	C. glauca	1990	N			
	C. obesa	1990	N			
Saudi Arabia	C. cristata	1982	N			
	C. cunninghamiana	1982	N			
	C. cunninghamiana X C. glauca	1982	N			
	C. equisetifolia	1997	N			
	C. glauca	1981	N			

	C. obesa	1986	N			
New Zealand						
New Zealand	C. cunninghamiana	1981	Y			
	C. equisetifolia	1982	N			
	C. glauca	1982	Y			
	C. grandis	1990	N			
	C. junghuhniana	1990	N			
North America						
USA (mainland)	C. collina	1997	N			
	C. cristata	1981	N			
	C. cunninghamiana	1924	Y*			
	C. equisetifolia	1825	Y*			
	C. glauca	1924	Y*			
	C. grandis	1988	N			
	C. junghuhniana	1984	N			
	C. obesa	1985	N			
	C. oligodon	1982	N			
Pacific Islands						
Hawaii	C. cunninghamiana		Y			
	C. equisetifolia	1882	Y*			
	C. glauca		Y*			
Ogasawara Archipelago	C. equisetifolia	1905	Y*			
South America						
Brazil	C. cristata	1981	N			
	C. cunninghamiana	1981	Y			
	C. equisetifolia	1984	Y			
	C. glauca	1981	N			

	C. junghuhniana	1984	N			
	C. oligodon	1984	N			
	C. pauper	1984	N			
Uruguay	C. cunninghamiana	1997	N			
	C. equisetifolia		N			

* Species known to be spreading.

Table S2.2 The number of citations of the most important *Casuarina* species in countries with significant plantings of casuarinas (15 geographical regions proposed by Richardson and Rejmánek 2011). Data were obtained from the annual indices of Forestry Abstracts (1966-2012) to give an index of the importance of different species

	C. collina	*C. cristata*	*C. cunninghamiana*	*C. equisetifolia*	*C. glauca*	*C. grandis*	*C. junghuhniana*	*C. obesa*	*C. oligodon*	*C. pauper*
Africa (rest)	0	2	51	124	65	0	6	4	1	0
Africa (Southern)	0	0	21	21	1	0	4	0	1	0
Asia	2	3	48	778	47	1	50	11	2	0
Atlantic Ocean Islands	0	1	1	4	0	0	0	0	0	0
Australia	0	42	80	48	42	0	0	21	0	9
Caribbean Islands	0	0	9	62	0	0	0	0	0	0
Central America	0	0	5	20	0	0	0	0	0	0
Europe	0	0	2	1	0	0	0	0	0	0
Indian Ocean Islands	0	0	2	15	0	0	0	0	0	0
Indonesia	0	0	0	39	1	0	11	0	6	0
Middle East	0	1	7	16	10	0	0	0	0	0

New Zealand	0	0	5	1	6	0	0	0	0	0
North America	0	0	27	29	23	0	0	0	0	0
Pacific Islands	4	0	8	39	6	0	0	0	0	0
South America	0	0	7	15	0	0	0	0	0	0
Total	**6**	**49**	**273**	**1212**	**201**	**1**	**71**	**36**	**10**	**9**

Table S2.3 The most important *Casuarina* species in countries with significant plantings of casuarinas (15 geographical regions proposed by Richardson and Rejmánek 2011). Data were obtained from the annual indices of Forestry Abstracts (1966-2012) to give an index of the importance of different species. Numbers in { } brackets after each country are the number of *Casuarina* citations for that region as a percentage of all *Casuarina* citations; this provides a crude index of the relative extent of the *Casuarina* plantations in that country (only countries with 0.1% of citations or more are listed – an additional 33 countries had less than 0.1% of citations). Numbers in ( ) brackets after each species are the number of citations for that species as a percentage of all *Casuarina* citations for that country. Numbers in [ ] brackets are the total number of *Casuarina* species cited for that country. Three species, *C. equisetifolia* (57%), *C. cunninghamiana* (13%) and *C. glauca* (8%) together account for almost 80% of all citations. Another seven species make up the remaining 20% of citations. No evidence was found for planting of *C. potamophila, C. tenella, C. teres,* and *C. tenuissima.*

Region & Country	***Casuarina* species**
Africa (rest)	
Algeria {0.1}	C. equisetifolia (33)
Benin {0.3}	C. equisetifolia (100)
Egypt {5.4}	C. glauca (48), C. cunninghamiana (36), C. equisetifolia (27), C. obesa (2)
Ethiopia {0.4}	C. equisetifolia (75), C. cunninghamiana (13), C. glauca (13)
Ivory Coast {0.1}	C. equisetifolia (67)
Kenya {1.5}	C. equisetifolia (71), C. junghuhniana (13), C. cunninghamiana (6), C. cristata (3), C. glauca (3), C. obesa (3), C. oligodon (3)
Morocco {0.3}	C. cunninghamiana (50), C. glauca (33)
Nigeria {0.5}	C. equisetifolia (70), C. cunninghamiana (10), C. glauca (10)
Senegal {1.6}	C. equisetifolia (94), C. junghuhniana (3)

Somalia {0.4}	C. equisetifolia (56)
Sudan {0.1}	C. equisetifolia (67), C. cristata (33), C. cunninghamiana (33), C. glauca (33), C. obesa (33)
Tunisia {0.5}	C. glauca (46), C. equisetifolia (18), C. cunninghamiana (9)
Uganda {0.2}	C. equisetifolia (80), C. cunninghamiana (20), C. junghuhniana (20)
Africa (Southern)	
Democratic Republic of Congo* {0.1}	C. equisetifolia (33)
Malawi {0.1}	C. equisetifolia (100)
Mozambique {0.1}	C. equisetifolia (67), C. cunninghamiana (33)
South Africa {0.8}	C. equisetifolia (44), C. cunninghamiana (31)
Swaziland {0.1}	C. cunninghamiana (100)
Tanzania {0.4}	C. equisetifolia (44), C. junghuhniana (44), C. cunninghamiana (22), C. oligodon (11)
Zambia {0.1}	C. cunninghamiana (100)
Zimbabwe {0.7}	C. cunninghamiana (57), C. equisetifolia (21), C. glauca (7)
Asia	
Bangladesh {0.5}	C. equisetifolia (90), C. cunninghamiana (10)
People's Republic of China {8.7}	C. equisetifolia (70), C. cunninghamiana (10), C. glauca (8), C. junghuhniana (8) [9]
India {30.6}	C. equisetifolia (79), C. junghuhniana (3), C. glauca (2), C. cunninghamiana (2), C. obesa (1) [6]
Japan {0.9}	C. equisetifolia (70), C. cunninghamiana (5), C. glauca (5)
Malaysia {0.8}	C. equisetifolia (88)
Nepal {0.2}	C. cunninghamiana (60), C. glauca (60), C. equisetifolia (20)

Pakistan {1.0}	C. equisetifolia (59), C. glauca (23), C. cunninghamiana (14), C. obesa (14)
Singapore {0.1}	C. equisetifolia (100)
Sri Lanka {0.5}	C. equisetifolia (33), C. cunninghamiana (20)
Republic of China (Taiwan) {3.4}	C. equisetifolia (67), C. glauca (11), C. junghuhniana (7), C. cunninghamiana (6), C. oligodon (1)
Thailand {1.9}	C. equisetifolia (49), C. junghuhniana (27), C. cunninghamiana (2)
Vietnam {0.9}	C. equisetifolia (68), C. cunninghamiana (11), C. glauca (5)
Atlantic Ocean Islands	
Bermuda {0.1}	C. equisetifolia (50)
Canary Islands (Spain) {0.1}	C. cunninghamiana (50)
Cape Verde Islands {0.1}	C. equisetifolia (100), C. cristata (33)
Australia	
Australia {14.2}	C. cunninghamiana (27), C. equisetifolia (16), C. cristata (14), C. glauca (14), C. obesa (7), C. pauper (3)
Caribbean Region	
Bahamas {0.2}	C. equisetifolia (25)
Costa Rica {0.5}	C. equisetifolia (60), C. cunninghamiana (50)
Cuba {1.8}	C. equisetifolia (81)
Jamaica {0.2}	C. cunninghamiana (75)
Puerto Rico {0.9}	C. equisetifolia (100)
Central America	
Guatemala {0.1}	C. equisetifolia (100), C. cunninghamiana (33)

Honduras {0.1}	C. equisetifolia (100), C. cunninghamiana (50)
Mexico {0.9}	C. equisetifolia (84), C. cunninghamiana (16)
Nicaragua {0.1}	C. equisetifolia (100)
Europe	
Spain {0.4}	C. cunninghamiana (11), C. equisetifolia (11)
Indian Ocean Islands	
Madagascar {0.2)	C. equisetifolia (25)
Mauritius {0.2}	C. equisetifolia (100)
Réunion Island (France) {0.4}	C. equisetifolia (75), C. cunninghamiana (25)
Seychelles {0.1}	C. equisetifolia (67)
Indonesia	
Indonesia {1.6}	C. junghuhniana (33), C. equisetifolia (21), C. oligodon (3)
Papua New Guinea {0.8}	C. equisetifolia (35), C. oligodon (29)
Philippines {1.4}	C. equisetifolia (87), C. glauca (3)
Middle East	
Iraq {0.3}	C. equisetifolia (71)
Israel {0.5}	C. cunninghamiana (50), C. glauca (50), C. cristata (10)
Jordan {0.1}	C. equisetifolia (100)
Saudi Arabia {0.5}	C. glauca (45), C. equisetifolia (36), C. cunninghamiana (18)
Yemen {0.2}	C. equisetifolia (80)

New Zealand	
New Zealand {0.9}	C. glauca (25), C. cunninghamiana (25), C. equisetifolia (5)
North America	
USA {4.6}	C. equisetifolia (30), C. cunninghamiana (28), C. glauca (24)
Pacific Islands	
Fiji {0.5}	C. equisetifolia (82)
Guam {0.1}	C. equisetifolia (100)
Hawaii (USA) {0.7}	C. equisetifolia (80), C. cunninghamiana (33), C. glauca (33)
New Caledonia {0.3}	C. collina (67)
Okinawa (Japan) {0.1)	C. equisetifolia (67), C. glauca (33)
Samoa {0.1}	C. equisetifolia (50)
Solomon Islands {0.1}	C. equisetifolia (100)
Vanuatu {0.2}	C. cunninghamiana (75), C. equisetifolia (50)
South America	
Argentina {0.4}	C. cunninghamiana (44), C. equisetifolia (11)
Brazil {0.4}	C. equisetifolia (75)
Chile {0.2}	C. equisetifolia (80), C. cunninghamiana (20)
Colombia {0.1}	C. equisetifolia (100)
Peru {0.1}	C. equisetifolia (33)
Uruguay {0.1}	C. cunninghamiana (50), C. equisetifolia (50)

Supplementary Figures

Figure S2.1 Predicted climatic suitability of the three most invasive *Casuarina* species: (a) *C. equisetifolia* (b) *C. cunninghamiana* (c) *C. glauca*. Shading indicates the number of species that could potentially grow (i.e. become naturalized) in different areas. Results are based on a bioclimatic analysis using a simple envelope approach using all *Casuarina* taxa. Predictions were generated using only climatic variables as inputs

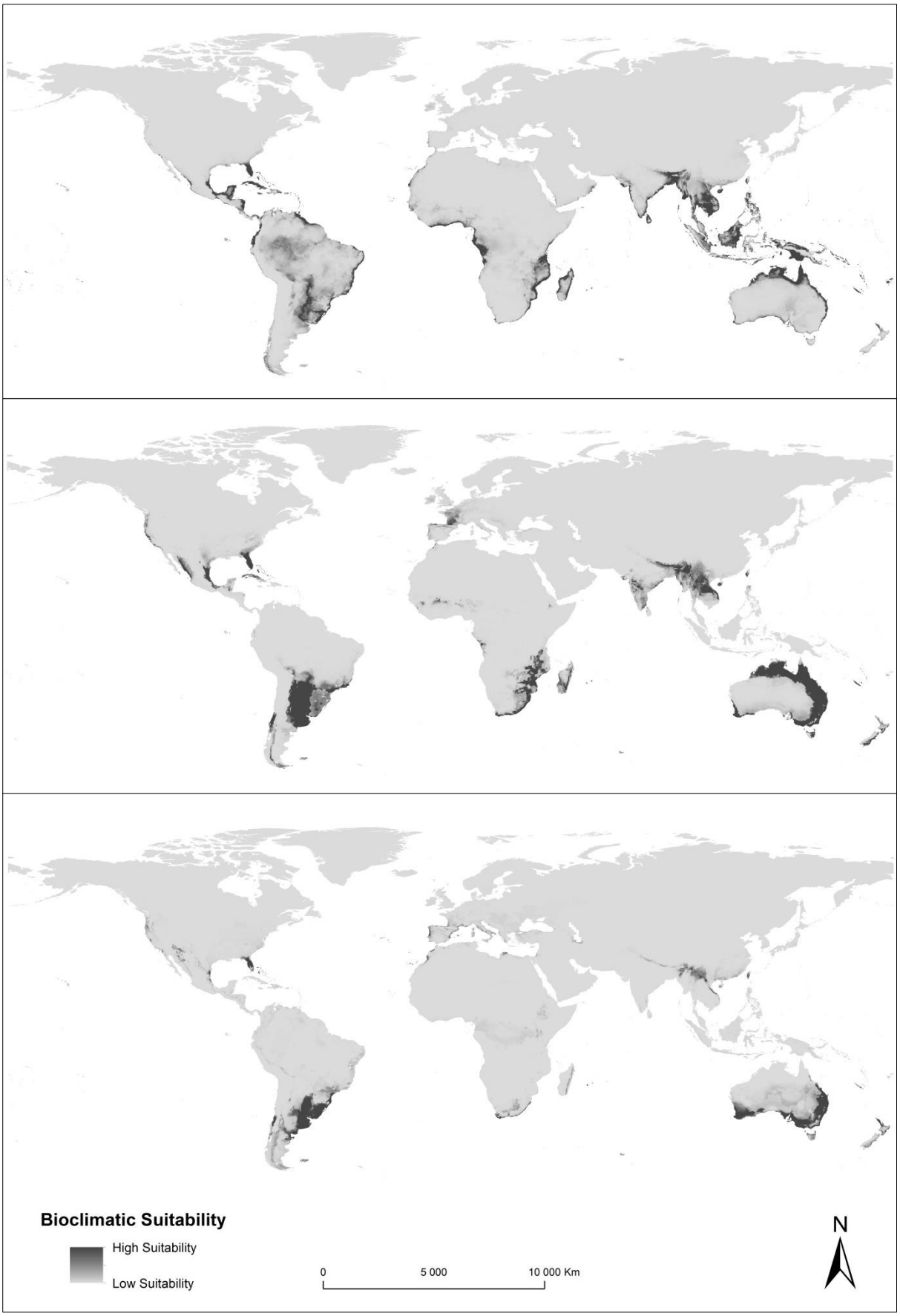

Figure S2.1

Chapter 3: *Casuarina cunninghamiana* in the Western Cape, South Africa: determinants of naturalization and invasion, and options for management

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LJP, DMR & JRUW: Planning and discussion of the study.
LJP: Database compilation, statistical analyses, led the writing.
DMR: Provided comments on the manuscript and improved the writing, and sourced species information for the database from international experts.
JRUW: Provided comments on the manuscript and statistical advice.

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3.1 Abstract

Alien species that are desirable and commercially important in some parts of the landscape but damaging invaders in other parts present a special challenge for managers, planners, and policy-makers. *Casuarina cunninghamiana* (Casuarinaceae), native to the eastern and north-eastern coasts of Australia, has been cultivated in South Africa for more than a century. This study explores the invasion ecology of *C. cunninghamiana* in the south-western part of the Western Cape. We examined differences between naturalized and non-naturalized populations (e.g. the roles of propagule pressure, land use and bioclimatic suitability), assessed invasion risk, and provide recommendations for control.

Naturalisation was observed at 81% of the populations surveyed. In climatically suitable areas, propagule pressure and distance to water bodies or water courses were significant predictors of naturalization - naturalization was most likely to occur within 100 m from the nearest planted individual and close to water bodies or water courses. The species has also naturalized in regions with suboptimal bioclimatic conditions, but then only very close (<10 m) to planted trees. Based on our findings we recommend: 1) the immediate removal of female trees from within 100 m of water bodies and or water courses; 2) all future sales and plantings to be restricted to male plants; and 3) the development of a management strategy (potentially including biological control) to control existing invasions and limit future spread. If these steps are taken, we believe it would be possible to maintain the beneficial uses the species has in some locations without incurring substantial negative impacts in other locations.

Keywords: Biological invasions, climatic suitability, naturalization, management, propagule pressure, risk mapping, tree invasions.

3.2 Introduction

Naturalization of alien plants is only achieved if they can overcome various barriers to establishment and reproduction. Invasion is contingent upon dispersal from introduction foci (Richardson et al., 2000). Successfully identifying traits correlated with invasiveness has direct application for the prediction of areas at risk of invasion and ultimately prevention of future invasions (Hulme, 2006), and considerable progress has been made towards understanding the determinants of invasiveness and invasibility (Rejmánek et al., 2004).

However, invasions remain difficult to predict because of the complex interactions between traits of the alien species, features of the environment, and the context in which they have been introduced and planted.

Invasive alien species, especially when the invasion is still at an early stage, are generally not at equilibrium with the environment (Richardson et al., 2010). At this stage, invasions are frequently more constrained by propagule availability than by habitat requirements (Rouget and Richardson, 2003; Donaldson et al., in press). Residence time and propagule pressure play an important role in structuring invasive plant populations (Lockwood et al., 2005; Wilson et al., 2007; Simberloff, 2009). Species introduced in large numbers over long periods have a greater chance of establishing and spreading than those with lower propagule pressure (Rouget and Richardson, 2003; Lockwood et al., 2005; Simberloff, 2009; Procheş et al., 2012).

Habitat suitability predictions have been used to identify areas at risk of invasions and predict spread pathways of invasive species so as to improve search and management strategies (Rouget et al., 2002; Richardson et al., 2010; Trethowan et al., 2011; Kaplan et al., 2014). Having a better idea of where to conduct intensive searches for a species could minimise the overall search area and reduce the risk of unattended invasions. As a result, highlighting areas with high suitability or risk of invasion by a species will improve the efficiency of searching and enable early detection of infestations before they are able to spread further.

Many introduced tree species are commercially important, but some have undesirable consequences in parts of their introduced ranges (Richardson et al., 2011). As more cultivated species become invasive and as the needs and perceptions of stakeholders become increasingly diverse, complex conflicts of interest often arise, and these may hinder management efforts (De Wit et al., 2011; van Wilgen et al., 2011; van Wilgen, 2012; Dickie et al., 2014; van Wilgen and Richardson, 2014).

A better understanding of the conflicts of interest and site-specific drivers of naturalization of an alien species can elucidate the associated invasion risks and ultimately provide an approach to risk management. This paper presents insights in this regard from a study of the invasion dynamics of *Casuarina cunninghamiana*.

3.2.1 History of Casuarina cunninghamiana in South Africa

The early introduction history of *C. cunninghamiana* in South Africa is complicated by the fact that the species was often confused with other species in the genus, particularly *C. equisetifolia*, *C. leptoclada* (now *Allocasuarina littoralis*) and *C. torulosa* (now *Allocasuarina torulosa*). Many accounts of *Casuarina* in South Africa do not identify the species or lump several species (e.g., Henderson, 2007; Poynton, 2009). Four seedlots identified as *C. cunninghamiana* were imported between 1902 and 1907 by the Cape and Transvaal colonial forest services, mostly from Australia. Arboretum trials were conducted under a range of climatic and edaphic conditions, and the species was used experimentally for fire belts in timber plantations (Poynton, 2009). Its potential in this regard was recognised as early as in the late nineteenth century. It received little attention as a forestry species, as it grows indifferently under plantation conditions, and is now predominantly cultivated for shade, shelter and ornament (Poynton, 1995; 2009).

Planted *Casuarina* species have become a conspicuous feature of many South African landscapes and have been economically important in many areas (Fig. 3.1). *Casuarina cunninghamiana* has been used extensively for shelterbelts, windbreaks and amenity purposes (Poynton, 1995). According to Molebatsi et al. (2010), *C. cunninghamiana* was one of ten species most commonly used for structural purposes in the North West Province, and occurred in more than 20% of home gardens. Trees of this species are often grown along vegetable gardens and houses to protect the crops and inhabitants from sand-laden winds. Fire screens made from branches are commonplace in areas without electricity and protect the outside cooking area from wind.

3.2.2 Invasion status of C. cunninghamiana in South Africa

Casuarina cunninghamiana was declared a category 2 invader by the Conservation of Agricultural Resources Act, 1983 (CARA; Henderson, 2001; Henderson, 2006). A demarcation permit is required to import, possess, grow, breed, move, sell, and buy the species. In addition, no permits are issued for planting of this species in riparian zones. Henderson (2007) records naturalization of *C. cunninghamiana* in savanna, grassland and fynbos biomes. Nel et al. (2004) classify this species as a “potential habitat transformer”. *Casuarina cunninghamiana* has a widespread distribution as a naturalized or invasive plant in South Africa, with populations occurring in Mpumalanga (4 quarter-degree grid cells -

QDCs), KwaZulu-Natal (3), Eastern Cape (3), and Gauteng (2), but it is most widespread in the Western Cape (11), particularly in the south-western parts of the province (7) (SAPIA, April 2013).

In its native range, *C. cunninghamiana* is typically the dominant plant in riparian habitats (Castle, 2008). It is restricted to river- and stream banks, and may extend for a short distance up rocky hillsides above watercourses (Orwa et al., 2009). In South Africa, river beds (Fig. 3.1d) and dams (Fig. 3.1g) are likely to act as conduits for seed dispersal via wind and water and provide microsites for seedling recruitment.

The overall extent of naturalization and invasion and the ecological impact of this species in South Africa remains poorly documented. With limited funds and resources available for invasive plant management, it is important to prioritise efforts based on the environmental and economic risks a species poses. An assessment of invasiveness, based on a species' biology and population dynamics, will provide a good indication of the risk posed by a species and inform plans for the species' management (Zenni et al., 2009; Moore et al., 2011). Highlighting areas with high suitability or risk of invasion by a species will thus improve the efficiency of searching and enable early detection of infestations before they are able to spread (Kaplan et al., 2014).

The capacity for resprouting and reaching reproductive age early, and its rapid growth rate and ability to fix nitrogen (Zhong et al., 2010) means that *C. cunninghamiana* could become a widespread and damaging invader in South Africa. This paper examines the distribution of planted versus naturalized individuals of *C. cunninghamiana* in one part of its range in South Africa – the southwestern part of the Western Cape. The study aims to: 1) assess factors that promote naturalization and invasion; 2) determine areas at risk of invasion by *C. cunninghamiana*; 3) provide guidelines for managing planted and naturalized populations to minimise the negative impacts resulting from invasion.

3.3 Methods and materials

3.3.1 Study species

Casuarina cunninghamiana Miq. (river she-oak; river oak; beefwood) is a tall, evergreen, nitrogen-fixing tree native to eastern Australia (Fig. 3.2a). It typically occurs in narrow belts along water streams and rivers.

The bark is finely fissured, scaly, and grey-brown. The branchlets are needle-like, 7.5 – 18 cm long, ca. 1 mm wide, with 8 – 10 lengthwise ridges ending in a ring of tiny, teeth-like scale leaves. The species has cone-like infructescences (Fig. 3.1a) but is not serotinous, with samaras (Fig. 3.1b) released when they are mature. Samaras are mostly distributed by wind close to female trees but are also carried by water. The cones are nearly round to elongate, 0.7 – 1.3 cm in diameter. It is dioecious, with individuals bearing unisex flowers (Fig. 3.1c) in an approximate 1:1 mix of both sexes.

Over the last century, *C. cunninghamiana* has been more widely disseminated than any other species in the genus, particularly to Africa, Asia, and to Central, South, and North America where it is used for many purposes (see Potgieter et al., 2014). It is the largest member of the genus and is adaptable to a wide range of conditions, and tolerates drought, periodic waterlogging, acid to moderately alkaline sandy to clay soils, and moderate levels of salinity. It is fast growing and seeds prolifically. It forms symbiotic associations with soil actinomycetes from the genus *Frankia* as well as ecto-, endo- and arbuscular mycorrhizal fungi (Diagne et al., 2013). Interspecific hybridization has been reported, which not only makes species identification difficult (Ho et al., 2002), but may contribute to invasion success (Gaskin et al., 2009). It is currently known to be naturalized in Argentina, Botswana, Brazil, Cyprus, Egypt, New Zealand, South Africa and Sudan (Rejmánek and Richardson, 2013), and is invasive in La Réunion Island (Kueffer and Lavergne, 2004; Baret et al., 2006) and Florida, USA, where it is considered among the worst invasive plants (Wheeler et al., 2011).

In South Africa, although fairly tolerant of frost, *C. cunninghamiana* thrives best in warm, humid to sub-humid climates (Poynton, 1995). However, it does not survive the low temperatures and lengthy droughts that occur in the colder, drier parts of the country without supplementary moisture (Poynton, 1995; 2009). Tolerant of poor drainage and mildly brackish conditions, it thrives on both clayey and sandy soils (Poynton, 1995). Nevertheless, it grows most vigorously on deep, moist but well aerated soil. In coastal areas it only tolerates indirect exposure to sea breezes. It is susceptible to herbivory by locusts and termites and seedlings are subject to browsing by stock (U.S. National Research Council, 1984). Naturalized populations occur in a variety of microhabitats in South Africa, including along rivers (Henderson, 2007) (Fig. 3.1d), disturbed areas such as roadsides (Fig. 3.1e), and periodically inundated (Fig. 3.1f) and submerged (Fig. 3.1f) areas. Naturalized individuals are able to resprout following treatment with fire (Fig. 3.1h) and after clearing (Fig. 3.1i).

3.3.2 Bioclimatic suitability

To estimate the potential distribution range of *C. cunninghamiana* in South Africa based on climate, we modelled the realised climatic niche of *C. cunninghamiana* using maximum entropy modelling (Maxent v. 3.3.3; Phillips et al., 2006) and projected it onto the current South African climate. The bioclimatic variables used to create the model were obtained from the WorldClim dataset (www.worldclim.org, Hijmans et al., 2005) at 5-minute resolution. We selected seven bioclimatic variables ('BioClim'): mean annual temperature (Bio1), isothermality (Bio3), temperature seasonality (Bio4), minimum temperature of the coldest month (Bio6), annual temperature range (Bio7), mean temperature of the driest quarter (Bio9), mean temperature of the coldest quarter (Bio11) and precipitation of the driest quarter (Bio17). Presence data for *C. cunninghamiana* were obtained from the Australian Virtual Herbarium (chah.gov.au/avh/; accessed 14 July 2012) for records from its native range, and from our own distribution data for the invasive range in South Africa. We fitted the model using all data, with duplicate records automatically removed from the analysis if more than one record existed per 5-min grid cell. Five hundred iterations of each model were conducted using the recommended default maximum number of background points (10,000) and convergence threshold (0.00001) (Phillips, 2006). We used a 10-fold cross-validation to estimate error around the average model fit and the average test area under curve (AUC) for model verification. We used the minimum training presence or lowest presence threshold (LPT; Pearson et al., 2007) to define climatically suitable areas. ASCII files of the binary prediction were opened in ArcMap and converted to Raster files for visual inspection of the distribution.

3.3.3 Study sites

We selected the south-western Cape as study area for assessing the invasion dynamics of this species as it is extensively used as a windbreak in agriculture in the region (Poynton, 1995), and there is a substantial climatically suitable range (Fig. 3.2b).

To locate *C. cunninghamiana* populations in the south-western Cape, we collated records from the Southern African Plant Invaders Atlas, SAPIA (Henderson, 1998) (accessed April 2013), the database of herbarium records (PRECIS, 2012), and an online spotter network (http://www.ispot.org.za/). Following detailed field searches we also added personal observations and information provided by farmers and land owners to the locality list. A

survey was conducted during August and September 2013 along ~950 km of roads in regions of the Western Cape where *C. cunninghamiana* is known to occur at high densities. Maximum speed was 40 km/h, with one person driving and one person searching for casuarinas. Every invaded site identified during the vehicle survey was searched on foot.

Our aim was to understand which site factors are important for triggering naturalization (i.e. the transition from introduction to naturalization; Richardson and Pyšek, 2012). A subset of QDCs were selected to include a variety of environmental conditions where *C. cunninghamiana* is known to succeed; these included different climatic conditions, hydrological patterns, land-use and soil types, management histories, native plant assemblages, and extent of planting (propagule pressure). We only conducted field surveys at sites where we thought populations may have a chance to spread (i.e. where plantings were established in potentially invasible habitats – see Moodley et al., 2013 for details). If spread was possible (i.e. if invasible habitats occurred in the vicinity of planted trees), we surveyed the site more carefully.

When conducting the road survey we observed numerous naturalized *C. cunninghamiana* populations on the edge of the largest dam in the region (the Theewaterskloof dam). This dam is bordered by cultivated land where C. cunninghamiana is widely planted as a windbreak. Preliminary observations found naturalized populations occurring far from planted populations, suggesting long-distance dispersal, almost certainly in water. For these reasons, we undertook an additional survey around the dam to determine the invasion dynamics of C. cunninghamiana in this special habitat (Box 3.1).

3.3.4 Population survey and reproductive size

The location of each plant was recorded using a handheld Global Positioning System (GPS Garmin® GPSMAP 602S). Each site was systematically surveyed on foot at least 10 metres from any plants observed. Naturalized (sensu Pyšek et al., 2004) individuals were categorised as seedlings (<30 cm in height); juveniles (>30 cm, non-reproducing plants); and mature adults (>30 cm, reproducing plants). At sites with abundant recruitment, the number of plants was estimated by walking around the population to delimit the extent of the population; placing transects through a part of the population that most accurately depicted the density and size classes; and counting all seedlings, juveniles and adults in the transect. The tracklogs from the tracking lines recorded in the GPS were used as the basis for drawing a polygon of

the surveyed area in Arcview GIS v.10.0. Planted individuals were mapped as ‘‘planted’’ where their position in the landscape clearly indicated planting by humans (e.g. regular pattern, proximity to picnic sites, roads, human settlements).

To determine age structure and size at reproduction, we measured the height of each plant, checked each plant for the presence of flowers and cones, and identified whether plants were resprouts. The significance of plant measurements in predicting the presence of reproductive structures was assessed using a generalised linear model, with a binomial error distribution, with signs of reproduction (0/1) as the response variable and height (log), as the predictor variable.

3.3.5 Potential distribution: planted vs. naturalized individuals

Identifying regions favourable to the survival and spread of invasive plants under different land-use and climatic conditions can help to understand where invasions may occur, so that steps can be taken toprevent invasion.

At each site, we assessed a variety of site-specific predictor variables (Table 3.1). These variables were selected based on the results of previous studies (Rouget and Richardson, 2002; Foxcroft et al., 2004; Moodley et al., 2013) that assessed the role of different factors in mediating plant naturalization in South Africa. The distribution of plantations and invasive stands of *C. cunninghamiana* were mapped and the data were digitised and stored as Geographic Information System (GIS) (Arc/Info) layers. Occurrence data were correlated with various environmental data using niche models to assess the suitable range for both planted and naturalized individuals separately.

The habitat suitability models were performed in three stages, first using all surveyed *C. cunninghamiana* populations (n=89), and second using populations in areas with suitable climatic conditions. Here, we found that a small proportion of populations occur in regions with suboptimal climates, which suggests that climate may serve as a barrier to naturalization. Therefore, we performed a final model using these populations to determine factors influencing naturalization in climatically unsuitable areas.

We used Maxent (following the same protocol used for the bioclimatic modelling) to relate the distribution of invasive stands with environmental variables, and to derive habitat suitability maps for future invasion. We used climatic, land use and topographic variables

that are known to influence the distribution of *C. cunninghamiana*, and variables related to history of the invasion to explain the distribution of naturalized individuals (Table 3.2). The climatic parameters used were: mean annual rainfall (*mar*), maximum summer temperature (*mst*), mean minimum annual temperature (*mmat*), and moisture availability (*mav*). Other variables used were: altitude (*alt*), distance to water bodies or water courses (*dwt*), distance to roads (*drd*), vegetation types (*veg*), national land cover (*lcov*), and natural soil pH (*spH*). Distance to water bodies or water courses was deemed useful since rivers and dams provide ideal sites for the establishment, growth and dispersal of this species (Fig. 3.1). Distance to the nearest planted individual (*dsp*) was also used to determine the importance of history in the naturalization of *C. cunninghamiana*.

To determine the distance at which naturalization is most likely to occur from the nearest planted individual, we tested the effect of distance to planted trees on naturalization at different distances for all surveyed populations; and populations in areas with suitable climatic conditions; and populations in areas with unsuitable climatic conditions: 50 m, 100 m, 200 m, 500 m, and 1000 m. Once the most significant distance had been identified, we tested the effects of all variables within this distance. The data were analysed using generalized linear models (GLMs) with binomial errors to test the significance of factors influencing the likelihood of populations naturalizing. The response variable was coded as '1' for naturalized populations and '0' for planted (non-naturalized) populations. All analyses were performed in R version 3.0.1 (R Development Core Team, 2010).

3.4 Results

3.4.1 Bioclimatic modelling

The model provided a good fit when projected back onto the native distribution of *C. cunninghamiana* in Australia: AUC=0.959 (sd±0.002). The logistic threshold that maximizes the sensitivity and the specificity values is 0.2179. When applying this threshold to South Africa, around 57% of the area of South Africa and 34% of the Western Cape has climatic conditions suitable for the growth (and possible invasion) of *C. cunninghamiana* – mostly in the north-eastern interior parts of the country and in the south-western Cape (Fig. 3.2). The bioclimatic variables that contributed most to the model results were isothermality, temperature seasonality, and mean annual precipitation which had relative contributions of 43.6%, 24.9% and 14.4% respectively.

3.4.2 Current distribution and population dynamics

Eighty-nine populations were surveyed: 72 that were naturalized (sensu Pyšek et al., 2004) and 17 where no evidence of naturalization was found. All naturalized sites contained a considerable proportion of small, immature plants, although plants of up to 15 m tall were recorded (Fig. 3.3a). There were substantial differences between sites in the size of plants at the onset of reproduction; 0.4 m was the minimum size observed for a reproductive plant and 32% of individuals taller than 1 m contained reproductive structures (Fig. 3.3b).

3.4.3 Areas prone to invasion by Casuarina cunninghamiana

Models were successful in generating both planted and naturalized present-day known distributions of *C. cunninghamiana* in the Western Cape (Table 3.2).

When all *C. cunninghamiana* populations were analysed, altitude and maximum summer temperature were important predictors for both naturalised and planted distribution (Table 3.2). However, planted distribution was also strongly predicted by distance to road, while the naturalised distribution was much more influenced by distance to water (Table 3.2). A similar trend was seen when only data from climatically suitable sites were considered. However, at sites predicted to be climatically unsuitable, moisture availability and distance to water sources were important variables for both planted and naturalised populations. When distance from naturalized individuals to planted trees (dsp) was added to each model estimating the distribution of naturalized individuals (NatDsp), dsp emerged as the most important and sole variable explaining the potential distribution of *C. cunninghamiana*.

Not surprisingly, the model 'planted' yielded a larger potential range of suitable conditions than naturalized (Fig. 3.4b, c, respectively). The models revealed that 29% of the Western Cape is at risk of invasion by *C. cunninghamiana*. Invasion risk is highest in climatically suitable areas, and areas that are close to sources of propagules and water bodies or water courses.

3.4.4 Site factors influencing the invasion status of Casuarina cunninghamiana

Naturalization was most likely to occur within 100 m from the nearest planted individual (F = 14.706, P < 0.0001, Table 3.3a). Within this distance, number of planted trees (F = 10.977, P = 0.002), altitude (F = 5.206, P = 0.003), soil pH (F = 4.947, P = 0.03) and land cover (F =

4.173, $P = 0.05$) were found to be associated with naturalization (Table 3.4a). Populations planted at higher altitudes had a greater probability of naturalizing. Naturalized *C. cunninghamiana* populations occurred mainly on neutral soils (pH 6.5 – 7.4) and planted populations were mostly present in slightly acidic soils (pH < 6.5). Naturalization occurred mainly on cultivated land.

In climatically suitable areas, naturalization was again most likely to occur within 100 m from the nearest planted individual ($F = 13.501$, $P < 0.001$, Table 3.3b). As with all *C. cunninghamiana* populations, number of planted trees ($F = 12.758$, $P < 0.001$), altitude ($F = 4.871$, $P < 0.03$), and land cover ($F = 4.840$, $P < 0.03$) were found to be associated with naturalization within this distance (Table 3.4b).

At climatically unsuitable sites, naturalization was most likely to occur within 10 m from the nearest planted individual - significantly less than in climatically suitable areas. Number of planted trees was the only variable found to be associated with naturalization in climatically unsuitable sites ($F = 9.321$, $P = 0.03$).

3.5 Discussion

Our results provide a clear example of the conditional nature of *C. cunninghamiana* invasions, with different factors driving naturalization at different sites. We were able to elucidate these factors and found that suitable climatic conditions, propagule pressure and distance to water bodies or water courses were strong determinants of naturalization, with naturalized populations occurring mostly in climatically suitable areas within 100 m from planted individuals. In suboptimal climatic conditions, naturalization only occurred very close (<10 m) to planted trees and water bodies or water courses. Our approach allows for the delineation of areas at risk of being invaded by *C. cunninghamiana* and provides a means of prioritizing search efforts by minimizing the total area that requires searching, thus increasing the probability of detecting a population before it is able to expand. Invasion risk is likely to be highest in areas that are climatically most suitable, and that are close (<100 m) to sources of propagules and water bodies or water courses. Our findings allow important management recommendations to be formulated. Despite a long residence time and high propagule pressure associated with *C. cunninghamiana*, the current stage structure (Fig. 3.3) of surveyed populations is indicative of young and expanding populations. In particular, a large number of seedlings are emerging, leading to a heavily skewed stage-structure. Although

cultivated land emerged as a significant determinant of naturalization in *C. cunninghamiana*, there is evidence that this species can naturalize in all areas where it is planted, particularly in sites close to water (Fig. 3.5). While it may simply be the time taken for numbers to build up combined with dispersal limitations, plants can reproduce when they are small and viable seeds are being produced in significant quantities (e.g. we recorded 5–10 seedlings/m^2 in some areas).

At two separate sites, windbreak plantings had experienced low-intensity fires. At the first site, 21% were unscathed and of those where the above-ground parts were killed, 66% resprouted from roots following the fire. At the second site, 76% remained unscathed while 7% of the dead individuals resprouted.

Invasion risk is likely to be highest in areas that are climatically most suitable, that are disturbed and that are in close proximity to sources of propagules (Richardson and van Wilgen, 2004). Proximity to propagule sources is intuitively an important factor influencing the spread of alien species into natural areas (Alston and Richardson, 2006).

In the absence of appropriate interventions, *C. cunninghamiana* is set to spread from its current distribution to invade a much larger area of the Western Cape. Propagule pressure proved a significant determinant of naturalization in climatically suitable areas. This suggests that if *C. cunninghamiana* is planted more widely in climatically suitable areas, populations would have the ability to successfully overcome barriers to naturalization. Human-mediated propagule pressure is therefore a crucial determinant of invasions, and any attempts to reduce further invasion of the species must address this factor.

Where the broad-scale climate is unsuitable, naturalization is limited to sites very close to planted trees and water bodies or water courses. Therefore, we predict that naturalizations in climatically unsuitable areas will not result in widespread invasive populations, which are likely to be fairly restricted and local.

In line with observations from its native and invasive range (Castle, 2008; Orwa et al., 2009), our risk model shows water bodies or water courses to be highly suitable for *C. cunninghamiana* establishment. Preliminary field observations from the Theewaterskloof dam (a focal site for invasion of this species in the Western Cape) showed that *C. cunninghamiana* establishes predominantly along the high-water mark on a variety of substrates and is able to survive periodic inundation (Box 3.1). Here, the distribution of

naturalized populations appears to be largely determined by propagule pressure and the direction of prevailing winds. Roadsides are also likely to be important for invasion of this species as they represent linear disturbances (Fig. 3.1e). Our risk model showed that disturbance associated with roadsides is moderately influential in predicting *C. cunninghamiana* environmental suitability (Table 3.2).

Maximum summer temperature was found to be influential in predicting both planted and naturalized *C. cunninghamiana* environmental suitability – areas with higher temperatures are less suitable. In its native range, *C. cunninghamiana* is mainly found in the warm sub-humid climatic zone with maximum temperature of the hottest month ranging from 25 to 40°C (Whistler and Elvitch, 2006). It is moderately drought resistant but is unable to tolerate semi-arid conditions unless additional water (irrigation or groundwater) is available to supplement rainfall (Orwa et al., 2009). Figure 3.1d shows how *C. cunninghamiana* is only able to spread in arid areas (>40°C during the summer months and <250 mm of rainfall per year) when additional water is provided or along water courses.

All indications are that this species is still at an early stage of invasion, and not at equilibrium with environmental conditions. Therefore, models calibrated using this limited set of occurrence data are likely to underestimate the potential naturalized distribution of *C. cunninghamiana* in the Western Cape and represent conservative predictions of the actual potential distribution of the species. The species is expected to expand its range when established individuals mature and act as new seed sources.

Considering that *C. cunninghamiana* is widely used as an agricultural windbreak, and that naturalization is most likely to occur within 100 m from the nearest planted individual, it is unsurprising that cultivated land proved an important determinant of naturalization. Naturalized populations of *C. cunninghamiana* were found mostly on neutral soils (pH 6.5 – 7.4) however, this species is able to tolerate acidic, neutral, alkaline and saline soils (Castle, 2008). With most naturalized populations occurring in cultivated areas, soil pH may fluctuate with the application of fertilizers.

Casuarina cunninghamiana invasions in the Western Cape can be categorised as widespread but not very abundant at any particular locality. However, there is a high potential for much greater spread and impact in future (Appendix 3.1). It is also clear that the species is widely utilised (summarised in Appendix 3.1). As such, management needs to reduce risk of future

spread, control existing invasions, and determine whether the invasion risk of its utilisation can be minimised.

Based on this concepts, we recommend that: 1) all future sales and plantings of *C. cunninghamiana* should be restricted to male plants; 2) all female plants (or if the sex cannot be determined, all plants) within 100 m of any water body or water course should be removed; and 3) a national management strategy be put in place to control current naturalized populations and limit their spread.

At a national scale, searching for *C. cunninghamiana* should be done within areas identified as having high climatic suitability for the species (Fig. 3.2b). Visser et al. (2014) have demonstrated the usefulness of Google Earth imagery for monitoring tree invasions and *C. cunninghamiana* could be a useful test case in this regard. As the agricultural industry is the most likely pathway for dissemination of this species and given the current association of *C. cunninghamiana* with plantations and water sources in its known invasive range, targeted awareness campaigns should be focussed particularly in these areas (Fig. 3.4c). If new invasions are found elsewhere in the country, a similar approach to searching at regional and local scales should be applied to detect all populations and plants within the affected area.

Given the current extent of invasion in the Western Cape and elsewhere in South Africa, eradication is not feasible. The goal for *C. cunninghamiana* management should be to limit spread where possible, and improve the efficacy of current management practices. The focus should be on a combination of mechanical, chemical and biological control in the high-risk areas proposed in this study. Given the strong ability of *C. cunninghamiana* to resprout, proper control and follow-up is essential to prevent re-establishment of dense stands and further spread.

We offer a few additional recommendations for future work to fully elucidate the risks and management options for the species in South Africa and to proactively reduce the likelihood of a major escalation of invasions. Firstly, a formal cost-benefit analysis should be undertaken at the national scale to assess the desirability and sustainability of using *C. cunninghamiana* as windbreaks. Secondly, landowners need to be made aware of the threat posed by *C. cunninghamiana*, and legal obligations relating to this species under CARA need to be strictly enforced. Thirdly, biological control has been considered for this species in Florida (Wheeler et al., 2011). While the species is not currently under consideration for

biocontrol in South Africa, and the current threat of invasion probably does not warrant the species being prioritised for South Africa to lead the development of biocontrol agents, agents that reduce the reproductive output could substantially reduce the risk of spread from plantings. The development of agents in the USA should be closely followed and supported if possible. If any promising agents are released, they should be considered for importation to South Africa.

If the proposed management recommendations discussed above are followed, it may be possible to utilise the species in an environmentally-friendly way in the future.

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References

AGIS, 2007. Agricultural Geo-Referenced Information System. www.agis.agric.za.

Alston, K.P., Richardson, D.M., 2006. The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. Biological Conservation 132, 183–198.

Baret, S., Rouget, M., Richardson, D.M., Lavergne, C., Egoh, B., Dupont, J., Strasberg, D., 2006. Current distribution and potential extent of the most invasive alien plant species on La Réunion (Indian Ocean, Mascarene Islands). Austral Ecology 31, 747-758.

Bennett, B.M., 2010. A global history of Australian trees. Journal of the History of Biology 44, 125-145.

Bennett, B.M., 2011. Naturalising Australian Trees in South Africa: Climate, Exotics and Experimentation. Journal of Southern African Studies 37, 225-280.

Brown, R.L., Chenoweth, J., 2008. The effect of Glines Canyon Dam on hydrochorous seed dispersal in the Elwha River. Northwest 18, 197–209.

Capon, S.J., Dowe, J.L., 2007. Diversity and dynamics of riparian vegetation. In: Lovett, S., Price, P. (Eds.), Principles for riparian lands management. Land & Water Australia, Canberra.

Castle, W.S., Langeland, K.A., Rockwood, D.L., 2008. *Casuarina cunninghamiana* Miq. (River sheoak) in Florida and its potential as a windbreak plant for citrus groves. *University* of *Florida's Cooperative Extension Service Publications* HS 1139.

Coetzee, J.A., Praglowski, J., 1984. Pollen evidence for the occurrence of *Casuarina* and *Myrica* in the Tertiary of South Africa. Grana 231, 23-41.

Department of Agriculture, Forestry and Fisheries (DAFF), 2009. Abstract of agricultural statistics. http://www.daff.gov.za

Diagne, N., Diouf, D., Svistoonoff, S., Kane, A., Noba, K., Franche, C., Bogusz, D., Duponnois, R., 2013. *Casuarina* in Africa: Distribution, role and importance of arbuscular mycorrhizal, ectomycorrhizal fungi and *Frankia* on plant development. Journal of Environ Management 128, 204-209.

Dickie, I.A., Bennett, B.M., Burrows, L.E., Nuñez, M.A., Peltzer, D.A., Porté, A., Richardson, D.M., Rejmanek, M., Rundel, P.W., van Wilgen, B.W. 2014. Conflicting values: ecosystem services and invasive tree management. Biological Invasions 16 (in press).

Donaldson, J.E., Hui, C., Richardson, D.M., Robertson, M.P., Webber, B.L., Wilson, J.R.U., (in press). Invasion trajectory of alien trees: the role of introduction pathway and planting history. Global Change Biology.

Doran, J., Hall, N., 1983. Notes on Fifteen Australian *Casuarina* species. In: Midgley, S.J., Turnbull, J., Johnston, R.D. (Eds.), *Casuarina* ecology, management and utilization. CSIRO, Australia, pp. 19-52.

Ellstrand, N.C., Schierenbeck, K.A., 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Proceedings of the National Academy of Science of the United States of America 97, 7043-7050.

Fenn, J.A., Kromhout, C., Coetzee, J., Maree, H.B., Von Gadow, K., 1973. Guide to Tree-Planting: Eastern Cape. The Department of Forestry, Pretoria.

Foxcroft, L.C., Rouget, M., Richardson, D.M., MacFadyen, S., 2004. Reconstructing 50 years of Opuntia stricta invasion in the Kruger National Park, South Africa: environmental determinants and propagule pressure. Diversity and Distributions 10, 427-437.

Galatowitsch, S.M., Anderson, N.O., Ascher, P.D., 1999. Invasiveness in wetland plants in temperate North America. Wetlands 19, 733–755.

Gaskin, J.F., Wheeler, G.S., Purcell, M.F., Taylor, G.S., 2009. Molecular evidence of hybridization in Florida's she-oak (*Casuarina* spp.) invasion. Molecular Ecology 18, 3216-3226.

Havel, J.E., Lee, C.E., Vander Zanden, M.J., 2005. Do reservoirs facilitate invasions into landscapes? BioScience 55, 518–525.

Henderson, L., 1998. Southern African Plant Invaders Atlas (SAPIA). Applied Plant Sciences 12, 31-32.

Henderson, L., 2001. Alien Weeds and Invasive Plants. Plant Protection Research Institute Handbook No. 12. Agricultural Research Council, Pretoria, pp. 1-300.

Henderson, L., 2006. Comparisons of invasive plants in southern Africa originating from southern temperate, northern temperate and tropical regions. Bothalia 36, 201-222.

Henderson, L., 2007. Invasive, naturalized and casual alien plants in southern Africa: a summary based on the Southern African Plant Invaders Atlas (SAPIA). Bothalia 37, 215-248.

Henderson, M., Fourie, D.M.C., Wells, M.J., Henderson, L., 1987. Declared weeds and alien invader plants in South Africa. Department of Agriculture and Water Supply, Pretoria.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25, 1965-1978.

Ho, K.-Y., Yang, J.C., Hsiao, J.Y., 2002. An assessment of genetic diversity and documentation of hybridization of *Casuarina* grown in Taiwan using RAPD markers. International Journal of Plant Science 163, 831–836.

Hulme, P.E., 2003. Biological invasions: winning the science battles but losing the conservation war? Oryx 37, 178-193.

Hulme, P.E., 2006. Beyond control: wider implications for the management of biological invasions. Journal of Applied Ecology 43, 835–847.

Hutchins, D.E., 1893. Tree-Planting, 1893 - A descriptive catalogue of the best trees to plant in Cape Colony, with brief instructions for planting. The Government Printer, Cape Town.

Iponga, D.M., Cuda, J.P., Milton, S.J., Richardson, D.M., 2008. Insect seed predation in *Schinus molle* (Peruvian pepper tree) differs with rainfall seasonality in South Africa: implications for invasiveness. African Entomology, 16, 127–131.

Kaplan, H., van Niekerk, A., Le Roux, J.J., Richardson, D.M., Wilson, J.R.U., 2014. Incorporating risk mapping at multiple spatial scales into eradication management plans. Biological Invasions, 16.

Keet, J.D.M., 1929. Tree planting in Orange Free State, Griqualand West, Bechuanaland and North-Eastern Districts of the Cape Province. Forest Department Bulletin No. 24., The Government Printer, Pretoria.

Kotze, P.C., 1929. Tree planting on the Natal North Coast Belt and in Zululand. The Government Printer, Pretoria.

Křivánek, M., Pyšek, P., Jarošík, V., 2006. Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. Conservation Biology 20, 1487–1498.

Kueffer, C., Lavergne, C., 2004. Case Studies on the Status of invasive Woody Plant Species in the Western Indian Ocean. 4. Réunion. Forest Health and Biosecurity Working Papers FBS/4-4E. Forestry Department, Food and Agriculture Organization of the United Nations, Rome, Italy.

Lockwood, J., Cassey, P., Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution 20, 223-8.

Low, A.B. Rebelo, A.G. (eds.) 1996. *Vegetation of South Africa, Lesotho and Swaziland*. Pretoria: DEAT.

Molebatsi, L.J., Siebert, S.J., Cilliers, S.S., Lubbe, C.S., Davoren, E., 2010. The Tswana tshimo: A homegarden system of useful plants with a particular layout and function. African Journal of Agricultural Research 5, 2952-2963.

Moodley, D., Geerts, S., Richardson, D.M., Wilson, J.R.U., 2013. Different traits determine introduction, naturalization and invasion success in woody plants: Proteaceae as a test case. PloS One 8(9), e75078. doi:10.1371/journal.pone.0075078

Moore, J.L., Runge, M.C., Webber, B.L., Wilson, J.R.U., 2011. Attempt to contain or eradicate? Optimising the management of Australian acacia invasions in the face of uncertainty. Diversity and Distributions 17, 1047-1059.

Mucina, L., Rutherford, M.C., 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia. South African National Biodiversity Institute, Pretoria.

Nel, J.L., Richardson, D.M., Rouget, M., Mgidi, T.N., Mdzeke, N., Le Maitre, D.C., van Wilgen, B.W., Schonegevel, L., Henderson, L., Neser, S., 2004. A proposed classification of invasive alien plant species in South Africa: towards prioritizing species and areas for management action. South African Journal of Science 100, 53-64.

New, T., Xie, Z.Q., 2008. Impacts of large dams on riparian vegetation: applying global experience to the case of China's Three Gorges Dam. Biodiversity and Conservation 17, 3149–3163.

Orwa, C., Mutua, A., Kindt, R., Jamnadass, R., Anthony, S., 2009. Agroforestree Database:a tree reference and selection guide version 4.0 (http://www.worldagroforestry.org/sites/treedbs/treedatabases.asp).

Pearson, R.G., Raxworthy, C.J., Nakamura, M., Peterson, A.T., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography, 34, 102-117.

Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences 11, 1633-1644.

Pheloung, P.C., Williams, P.A., Halloy, S.R., 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. Journal of Environmental Management 57, 239-251.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190, 231-259.

Potgieter, L.J., Richardson, D.M., Wilson, J.R.U. 2014. *Casuarina*: biogeography and ecology of an important tree genus in a changing world. Biological Invasions 16 (in press).

Poynton, R.J., 1995. Report to the Southern African Regional Commission for the Conservation and Utilization of the Soil (SARCCUS) on tree planting in southern Africa. Vol. 1. Other Genera - *Casuarina*. Department of Forestry, South Africa.

Poynton, R.J., 2009. Tree planting in Southern Africa. Volume 3: other genera, Department of Agriculture, Forestry and Fisheries, Pretoria.

PRECIS, 2012. National Herbarium Pretoria (PRE) Computerised Information System. http://posa.sanbi.org/intro_precis.php.

Procheş, Ş., Wilson, J.R.U., Richardson, D.M., Rejmánek, M., 2012. Native and naturalized range size in *Pinus*: relative importance of biogeography, introduction effort and species traits. Global Ecology and Biogeography 21, 513–523.

Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G., Williamson, M., Kirschner, J., 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53, 131-143.

R Development Core Team., 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rejmánek, M., Richardson, D.M., 2013. Trees and shrubs as invasive alien species - 2013 update of the global database. Diversity and Distributions 19, 1093-1094.

Rejmánek, M., Richardson, D.M., Higgins, S.I., Pitcairn, M.J., Grotkopp, E., 2005. Ecology of invasive plants - state of the art. In: Mooney, H.A., Mack, R.N., Mc Neely, J.A., Neville, L., Schei, P.J., Waage, J. (Eds.), Invasive alien species: A new synthesis, pp. 104-161. Island Press, Washington D.C.

Richardson, D., Pyšek, P., 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography 30, 409-431.

Richardson, D.M., 2006. *Pinus*: a model group for unlocking the secrets of alien plant invasions? Preslia 78, 375-388.

Richardson, D.M., Cambray, J.A., Chapman, R.A., Dean, W.R.J., Griffiths, C.L., Le Maitre, D.C., Newton, D.J., Winstanley, T.J., 2003. Vectors and pathways of biological invasions in South Africa – past, future and present. In: Ruiz, G., Carlton, J. (Eds.), Invasive Species: Vectors and Management Strategies. Island Press, Washington, DC, pp. 292–349.

Richardson, D.M., Iponga, D.M., Roura-Pascual, N., Krug, R.M., Milton, S.J., Hughes, G.O., Thuiller, W., 2010. Accommodating scenarios of climate change and management in modelling the distribution of the invasive tree *Schinus molle* in South Africa. Ecography 33, 1049-1061.

Richardson, D.M., Pyšek, P., 2012. Naturalization of introduced plants: ecological drivers of biogeographical patterns. New Phytologist 196, 383-396.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, D.F., West, C.J., 2000. Naturalization and invasion of alien plants - concepts and definitions. Diversity and Distributions 6, 93-107.

Richardson, D.M., Rejmánek, M., 2011. Trees and shrubs as invasive alien species - a global review. Diversity and Distributions 17, 788-809.

Richardson, D.M., van Wilgen, B.W., 2004. Invasive alien plants in South Africa: how well do we understand the ecological impacts? South African Journal of Science 100, 45–52.

Roberts, J., Marston, F., 2011. Water regime for wetland and floodplain plants. A source book for the Murray-Darling Basin. National Water Commission, Canberra.

Rouget, M., Richardson, D.M., 2003. Inferring process from pattern in alien plant invasions: a semi-mechanistic model incorporating propagule pressure and environmental factors. American Naturalist 164, 713-724.

Rouget, M., Richardson, D.M., Nel, J.A., van Wilgen, B.W., 2002. Commercially-important trees as invasive aliens - towards spatially explicit risk assessment at a national scale. Biological Invasions 4, 397-412.

Rouget, M., Richardson, D.M., Nel, J.L., Le Maitre, D.C., Egoh, B., Mgidi, T., 2004. Mapping potential distribution of major invaders in South Africa, Lesotho and Swaziland using climatic suitability. Diversity and Distributions 10, 475-484.

Sim, T.R., 1921. *Native Timbers of South Africa.* The Government Printer, Pretoria.

Simberloff, D., 2009. The role of propagule pressure in biological invasions. *Annual Review* of *Ecology, Evolution,* and Systematics 40, 81–102.

Swain, V.M., Prinsloo, G.L., 1986. A list of phytophagous insects and mites on forest trees and shrubs in South Africa. Entomology Memoir No. 66. Department of Agriculture and Water Supply, Pretoria.

Swanepoel, D., Underhill, L.G., Harebottle, D.M., Wheeler, M.J., Williams, A.J., 2006. Waterbirds at the Theewaterskloof Dam, Western Cape, South Africa, 1993–2005. Ostrich 77, 170–174.

Thompson, G.D., Robertson, M.P., Webber, B.L., Richardson, D.M., Le Roux, J.J., Wilson, J.R.U., 2011. Predicting the sub-specific identity of invasive species using distribution models: *Acacia saligna* as an example. Diversity and Distributions 17, 1001-1014.

Trethowan, P.D, Robertson, M.P., McConnachie, A.J., 2011. Ecological niche modelling of an invasive alien plant and its potential biological control agents. South African Journal of Botany 77, 137-146.

U.S. National Research Council, 1984. Casuarinas: Nitrogen-fixing trees for adverse sites. National Academy Press, Washington D.C.

van Wilgen, B.W., 2012. Evidence, perceptions, and trade-offs associated with invasive alien plant control in the Table Mountain National Park, South Africa. Ecology and Society 17(2), 23.

van Wilgen, B.W., Dyer, C., Hoffmann, J.H., Ivey, P., Le Maitre, D.C., Moore, J.L., Richardson, D.M., Rouget, M., Wannenburgh, A., Wilson, J.R.U., 2011. National-scale strategic approaches for managing introduced plants: insights from Australian acacias in South Africa. Diversity and Distributions 17, 1060–1075.

van Wilgen, B.W., Richardson, D.M., 2014. Managing invasive alien trees: challenges and trade-offs. Biological Invasions 16 (in press).

Visser, V., Langdon, B., Pauchard, A., Richardson, D.M., 2014. Unlocking the potential of Google Earth as a tool in invasion science. Biological Invasions 16 (in press)

Webber, B.L., Yates, C.J., Le Maitre, D.C., Scott, J.K., Kriticos, D.J., Ota, N., McNeill, A., Le Roux, J.J., Midgley, G.F., 2011. Modelling horses for range-shifting courses: projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models. Diversity and Distributions 17, 978-1000.

Wheeler, G.S., Taylor, G.S., Gaskin, J.F., Purcell, M.F., 2011. Ecology and management of Sheoak (*Casuarina* spp.), an invader of coastal Florida, USA. Journal of Coastal Research 27, 485-492.

Whistler, W.A., Elevitch, C.R., 2006. *Casuarina equisetifolia* (reach she-oak) and *C. cunninghamiana* (river she-oak), ver. 2.1. In: Elevitch, C.R. (Ed.), Species Profiles for Pacific Island Agroforestry. Permanent Agriculture Resources (PAR), Hōlualoa, Hawai‘i. http://www.traditionaltree.org.

Wilson J.R.U., Richardson D.M., Rouget, M., Procheş, Ş., Amis, M.A., Henderson, L., Thuiller, W., 2007. Residence time and potential range: crucial considerations in modelling plant invasions. Diversity and Distributions 13, 11-22.

Wilson, J.R.U., Caplat, P., Dickie, I., Hui, C., Maxwell, B.D., Nuñez, M.A., Pauchard, A., Rejmánek, M., Richardson, D.M., Robertson, M.P., Spear, D., Webber, B.L., van Wilgen, B.W., Zenni, R.D., 2014. A standardized set of metrics to assess and monitor tree invasions. Biological Invasions 16 (in press).

Wilson, J.R.U., Gairifo, C., Gibson, M.R., Arianoutsou, M., Bakar, B.B., Baret, S., Celesti-Grapow, L., Dufour-Dror, J.M., Kueffer, C., Kull, C.A., Hoffmann, J.H., Impson, F.A.C., Loope, L.L., Marchante, E., Marchante, H., Moore, J.L., Murphy, D., Pauchard, A., Tassin, J., Witt, A., Zenni, R.D., Richardson, D.M., 2011. Risk assessment, eradication, containment, and biological control: global efforts to manage Australian acacias before they become widespread invaders. Diversity and Distributions 17, 1030-1046.

Woolfrey, A.R., Ladd, P.G., 2001. Habitat preference and reproductive traits of a major Australian riparian tree species (*Casuarina cunninghamiana*). Australian Journal of Botany 49, 705-15.

Zenni, R.D., Wilson, J.R.U., Le Roux, J.J., Richardson, D.M., 2009. Evaluating the invasiveness of *Acacia paradoxa* in South Africa. South African Journal of Botany 75, 485-496.

Zhong, C., Zhang, Y., Chen, Y., Chen, Z., Jiang, Q., Pinyopusarerk, K., Franche, C., 2010. Potential *Casuarina* species and suitable technology for the GGW. In: Dia, A., Duponnois, R., Wade, A. (Eds.), The major project of the African Great Green Wall: Concepts and implementation. IRD, Marseille, pp 163-170.

Tables

Table 3.1. Variables used to develop a model to predict the potential distribution for *Casuarina cunninghamiana* in the south-western part of the Western Cape, South Africa and the methods of measurement used.

Predictor variable	Methods of measuring	Categories	Reference
Altitude	GPS	Continuous	
Distance to nearest planted individual	Euclidean distance using Spatial Analyst tool in ArcMap	Continuous	
Distance to roads	Euclidean distance using Spatial Analyst tool in ArcMap	Continuous	
Distance to water	Euclidean distance using Spatial Analyst tool in ArcMap	Continuous	
Land cover	Land types adjacent to populations	Categorical	AGIS, 2007
Management	Whether plants are cut or irrigated	Categorical, binary	
Maximum summer temperature			AGIS, 2007
Mean annual rainfall			AGIS, 2007
Mean minimum annual temperature			AGIS, 2007
Moisture availability			AGIS, 2007
Propagule pressure	Total number of planted individuals	Continuous	
Soil pH	Weighted average of pH values	Categorical	AGIS, 2007

Vegetation types	Categorical	Mucina and Rutherford, (2006)

Table 3.2. The relative influence of variables used to predict environmental suitability for *Casuarina cunninghamiana*. NatDsp = model built when adding the variable distance to the nearest planted individual. AUC is the area under the curve of the Receiver Operator Characteristic.

Model	**Variables relative influence (%)**											**AUC**
	Mean annual rainfall	Moisture availability	Max. Summer temperature	Mean minimum annual temperature	Altitude	Distance to water sources	Distance to roads	Vegetation types	National land cover	Natural soil ph	Distance to the nearest planted individual	
All sites												
Planted	6.0	8.5	**11.2**	1.5	**25.6**	4.1	**25.9**	6.5	3.1	7.6	-	0.965
Naturalized	5.0	3.2	**13.6**	3.2	**42.8**	**10.0**	4.6	7.1	0.7	9.9	-	0.982
NatDsp	0.0	0.1	0.1	0.1	0.4	0.0	0.0	0.0	0.0	0.0	**99.2**	0.992
Climatically suitable sites only												
Planted	4.8	6.5	**23.3**	2.6	**14.3**	**18.0**	**16.2**	7.6	0.9	5.9	-	0.982
Naturalized	3.0	4.6	**16.5**	2.1	**23.6**	**23.2**	**10.5**	8.9	1.0	6.6	-	0.984
NatDsp	0.0	0.0	0.2	0.1	0.1	0.1	0.0	0.0	0.0	0.0	**99.5**	0.995

Climatically unsuitable sites only												
Planted	4.4	**13.3**	2.9	0.8	0.0	**37.6**	**35.2**	1.1	3.5	1.2	-	0.996
Naturalized	3.6	**20.1**	**10.0**	0.1	0.9	**30.8**	**19.0**	**10.4**	2.5	2.6	-	0.982
NatDsp	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	1.8	**97.8**	0.999

Table 3.3. Linear regressions of the factors influencing naturalization of *Casuarina cunninghamiana* populations in South Africa. (a) All surveyed populations (n=89); (b) populations in areas with suitable climatic conditions (n=75). Median and range of the data are given for continuous variables.

(a)

Variable	Median, range	Test	Relationship
Altitude	197, 19 – 410	F = 0.606321, P = 0.438289	No effect
Arable land		F = 0.171263, P = 0.680010	No effect
Deep sand		F = 0.669725, P = 0.415384	No effect
Distance to dams (m)	460, 0.1 – 2865	F = 1.061853, P = 0.305649	No effect
Distance to plantings (m)	363, 0.1 – 20919	F = 14.706, P = 0.000257	Naturalization is most likely to occur within 100 m from the nearest planted individual
Distance to rivers (m)	1329, 0.7 – 4220	F = 0.150779, P = 0.698741	No effect
Distance to roads (m)	257, 1.7 – 2296	F = 0.208332, P = 0.649216	No effect
Dry land		F = 0.096454, P = 0.756871	No effect
Habitation		F = 0.149277, P = 0.700170	No effect
Land cover		F = 0.203413, P = 0.653102	No effect

Management		$F = 0.504063$, $P = 0.479619$	No effect
Moisture availability		$F = 0.034947$, $P = 0.852142$	No effect
Number of planted individuals (log transformed)	220, 0 – 1050	$F = 0.917676$, $P = 0.340740$	No effect
Pastoral land		$F = 0.027038$, $P = 0.869771$	No effect
Road/rail		$F = 0.020218$, $P = 0.887257$	No effect
Rocky		$F = 0.035164$, $P = 0.851689$	No effect
Soil pH	7, 5.5 – 7.5	$F = 4.946886$, $P = 0.028727$	More neutral soils favour naturalization
Transformed		$F = 0.601701$, $P = 0.440033$	No effect
Vegetation type		$F = 1.333573$, $P = 0.251333$	No effect
Wasteland		$F = 0.173544$, $P = 0.678007$	No effect

(b)

Variable	**Median, range**	**Test**	**Relationship**
Altitude	195, 19 – 410	$F = 0.470236$, $P = 0.495051$	No effect
Arable land		$F = 0.214689$, $P = 0.644495$	No effect

Deep sand		$F = 0.506433$, $P = 0.478955$	No effect
Distance to dams (m)	429, 0 – 2865	$F = 0.918953$, $P = 0.340914$	No effect
Distance to plantings (m)	363, 0.1 – 20919	$F = 0.044958$, $P = 0.000499$	Naturalization is most likely to occur within 100 m from the nearest planted individual
Distance to rivers (m)	1317, 0.7 – 4096	$F = 0.702259$, $P = 0.702259$	No effect
Distance to roads (m)	276, 1.7 – 2296	$F = 0.250716$, $P = 0.618078$	No effect
Dry land		$F = 0.028562$, $P = 0.866262$	No effect
Habitation		$F = 0.179441$, $P = 0.673100$	No effect
Land cover		$F = 0.087661$, $P = 0.768013$	No effect
Management		$F = 0.519106$, $P = 0.473524$	No effect
Moisture availability		$F = 0.060602$, $P = 0.806238$	No effect
Number of planted individuals (log transformed)	233, 0 – 1050	$F = 0.676604$, $P = 0.413438$	No effect
Pastoral land		$F = 0.032453$, $P = 0.857537$	No effect
Road/rail		$F = 0.018397$, $P = 0.892484$	No effect
Rocky		$F = 0.009994$, $P = 0.920642$	No effect

Soil pH	7, 5.5 – 7.5	F = 13.50136, P = 0.056551	No effect
Transformed		F = 0.452129, P = 0.503449	No effect
Vegetation type		F = 2.307511, P = 0.133069	No effect
Wasteland		F = 0.183273, P = 0.669836	No effect

Table 3.4. Linear regressions of the factors influencing naturalization of *Casuarina cunninghamiana* populations in South Africa within 100 m of the nearest planted individual. (a) All surveyed populations (n=89); (b) populations in areas with suitable climatic conditions (n=78). Median and range of the data are given for continuous variables.

(a)

Variable	Median, range	Test	Relationship
Altitude	186, 19 – 361	$F = 5.208$, $P = 0.026869$	Populations at the higher altitudinal range have a greater probability of naturalizing
Arable land		$F = 0.20842$, $P = 0.650028$	No effect
Deep sand		$F = 0.00261$, $P = 0.959432$	No effect
Distance to dams (m)	478, 0.1 – 2865	$F = 0.08557$, $P = 0.771118$	No effect
Distance to plantings (m)	12, 0.1 – 91	$F = 11.51218$, $P = 0.001315$	Naturalization is most likely within 100 m of the nearest planted individual
Distance to rivers (m)	1350, 0.7 – 4220	$F = 0.00953$, $P = 0.922649$	No effect
Distance to roads (m)	235, 5.4 – 2296	$F = 2.13909$, $P = 0.149972$	No effect
Dry land		$F = 0.00015$, $P = 0.990318$	No effect
Habitation		$F = 0.04701$, $P = 0.829247$	No effect
Land cover		$F = 4.17309$, $P = 0.046469$	Naturalization is more likely to occur on

			cultivated land
Management		F = 1.08963, P = 0.301677	No effect
Moisture availability		F = 2.84668, P = 0.097920	No effect
Number of planted individuals (log transformed)	236, 0 – 1050	F = 10.977, P = 0.001740	Higher propagule pressure is more likely to result in naturalization
Pastoral land		F = 0.01662, P = 0.897953	No effect
Road/rail		F = 1.58370, P = 0.214192	No effect
Rocky		F = 0.00663, P = 0.935418	No effect
Soil pH	7, 5.5 – 7.5	F = 4.55059, P = 0.037941	More neutral soils favour naturalization
Transformed		F = 0.38768, P = 0.536408	No effect
Vegetation type		F = 0.02424, P = 0.876917	No effect
Wasteland		F = 0.03097, P = 0.861033	No effect

(b)

Variable	**Median, range**	**Test**	**Relationship**
Altitude	181, 19 – 361	F = 4.87088, P = 0.033965	No effect

Arable land		$F = 0.20726$, $P = 0.651735$	No effect
Deep sand		$F = 0.00003$, $P = 0.996034$	No effect
Distance to dams (m)	458, 0 – 2865	$F = 0.17849$, $P = 0.675258$	No effect
Distance to plantings (m)	12, 0.1 – 91	$F = 12.17413$, $P = 0.001194$	Naturalization is most likely to occur within 100m of the nearest planted individual
Distance to rivers (m)	1341, 0.7 – 4096	$F = 0.01445$, $P = 0.904993$	No effect
Distance to roads (m)	252, 5.4 – 2296	$F = 2.20371$, $P = 0.146630$	No effect
Dry land		$F = 0.14799$, $P = 0.702794$	No effect
Habitation		$F = 0.16806$, $P = 0.684336$	No effect
Land cover		$F = 4.84035$, $P = 0.034494$	Naturalization is more likely to occur on cultivated and/or degraded land
Management		$F = 1.60647$, $P = 0.213357$	No effect
Moisture availability		$F = 3.31237$, $P = 0.077321$	No effect
Number of planted individuals (log transformed)	256, 0 – 1050	$F = 12.75844$, $P = 0.001055$	No effect
Pastoral land		$F = 0.00527$, $P = 0.942558$	No effect
Road/rail		$F = 2.12696$, $P = 0.153643$	No effect

Rocky		$F = 0.00271$, $P = 0.958744$	No effect
Soil pH	7, 5.5 – 7.5	$F = 3.77158$, $P = 0.060213$	No effect
Transformed		$F = 0.65342$, $P = 0.424353$	No effect
Vegetation type		$F = 0.03187$, $P = 0.859349$	No effect
Wasteland		$F = 0.11089$, $P = 0.741125$	No effect

Figures

Fig. 3.1. *Casuarina cunninghamiana* in the Western Cape, South Africa. (a) The species in full flower (male), (b) female cones each containing hundreds of (c) samaras, (d) spreading along roadsides or disturbed sites adjacent to roads, (e) planted as windbreaks for citrus orchards and spreading into the adjacent river (note active management), (f) naturalized in a periodically inundated area, (g) naturalized in a farm dam, which is at full capacity only after the rainy season (adult trees survive periodic inundation and juveniles survive periodic submersion), (h) naturalized individual resprouting following treatment with fire, (i) resprouting after clearing. (All photos: L.J. Potgieter)

Fig. 3.2. Predicted climatic suitability of *Casuarina cunninghamiana* in (a) its native range in Australia with native distribution records and (b) in South Africa. Native distribution data was obtained from the Atlas of Living Australia, http://www.ala.org.au.

Fig. 3.3. a) Plant height frequency distributions; and b) size at reproduction for *Casuarina cunninghamiana*. The frequency distributions were produced using the function density [stats] in R. The presence of cones or flowers was used as proxy for reproductive maturity with some jitter added to prevent over plotting. The fitted line for each site is from a generalised linear model with binomial errors and log (plant height) as the explanatory variable.

Fig. 3.4. a) Risk map for *Casuarina cunninghamiana* in the Western Cape, South Africa, modelled using locations of planted and naturalized individuals. Maps show (a) the roads surveyed, and the current predicted suitability for (b) planted and (c) naturalized individuals.

Fig. 3.5. The major land use types of all naturalized and non-naturalized *Casuarina cunninghamiana* populations in the Western Cape, South Africa. Habitation refers to populations planted in farm yards and gardens, transformed land is dominated by invasive alien plants, pastoral land includes areas used for farming with domestic or wild animals, and wasteland refers to abandoned land, dumping sites, quarries or eroded land.

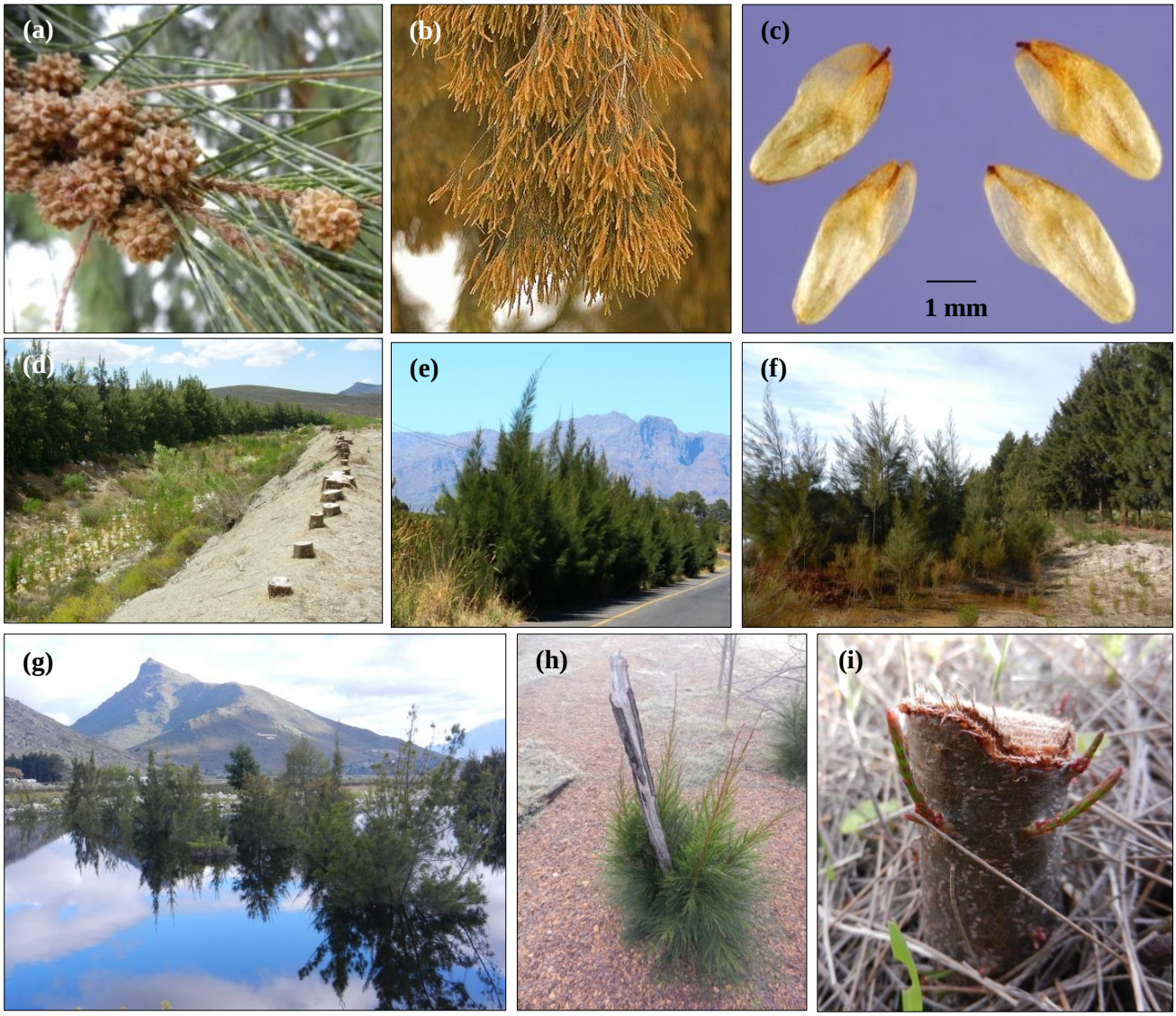


Figure 3.1.

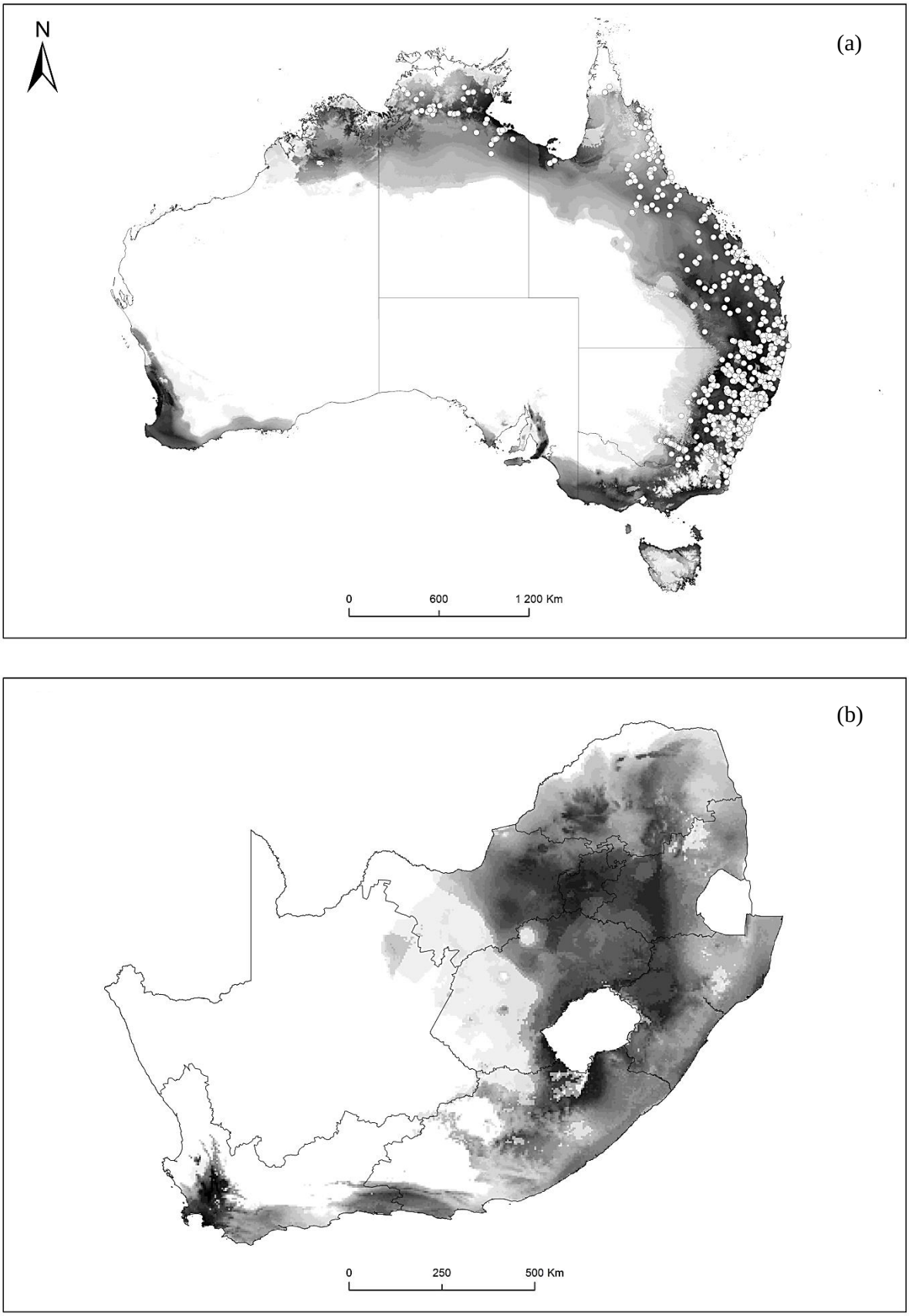


Figure 3.2.

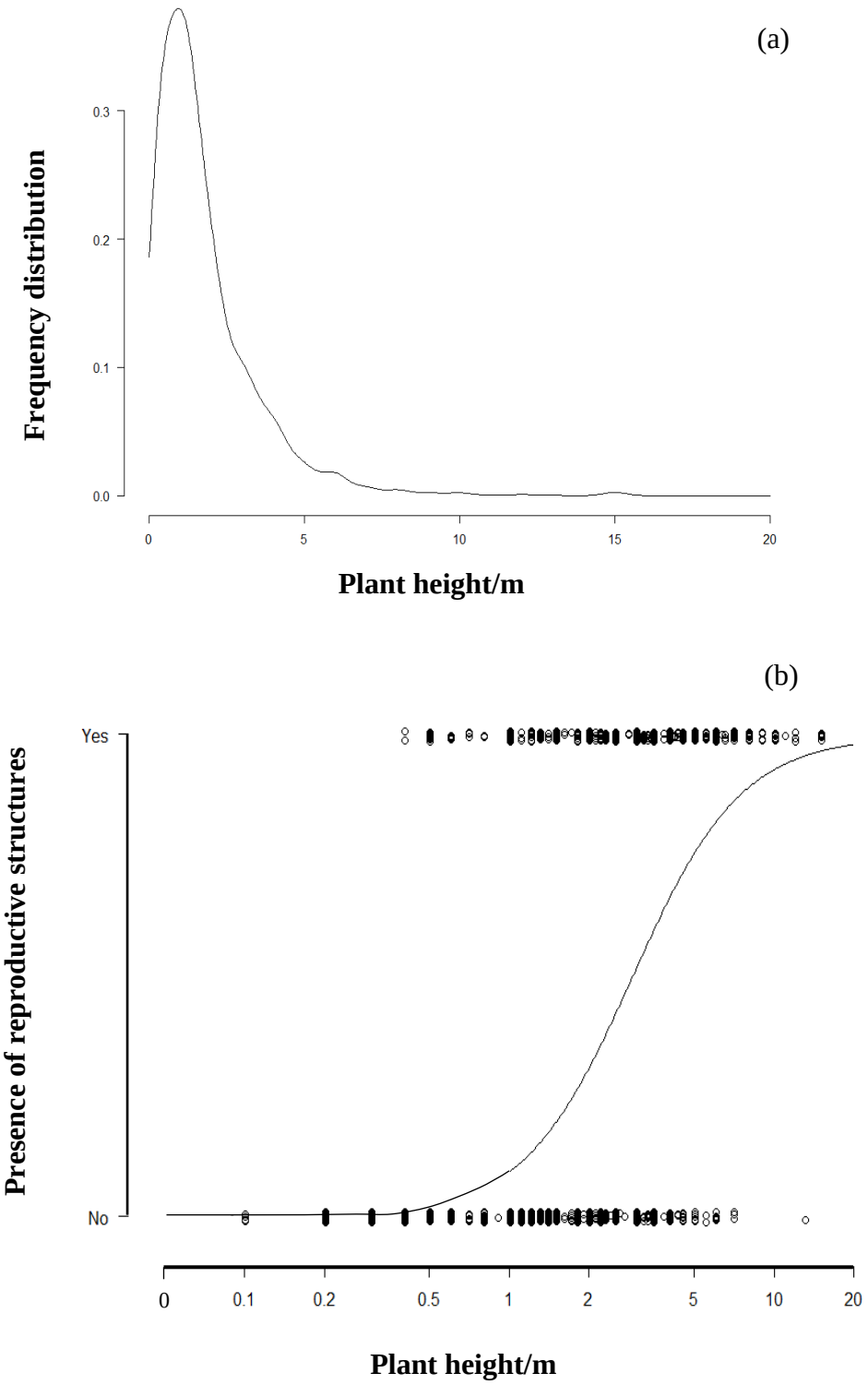


Figure 3.3.

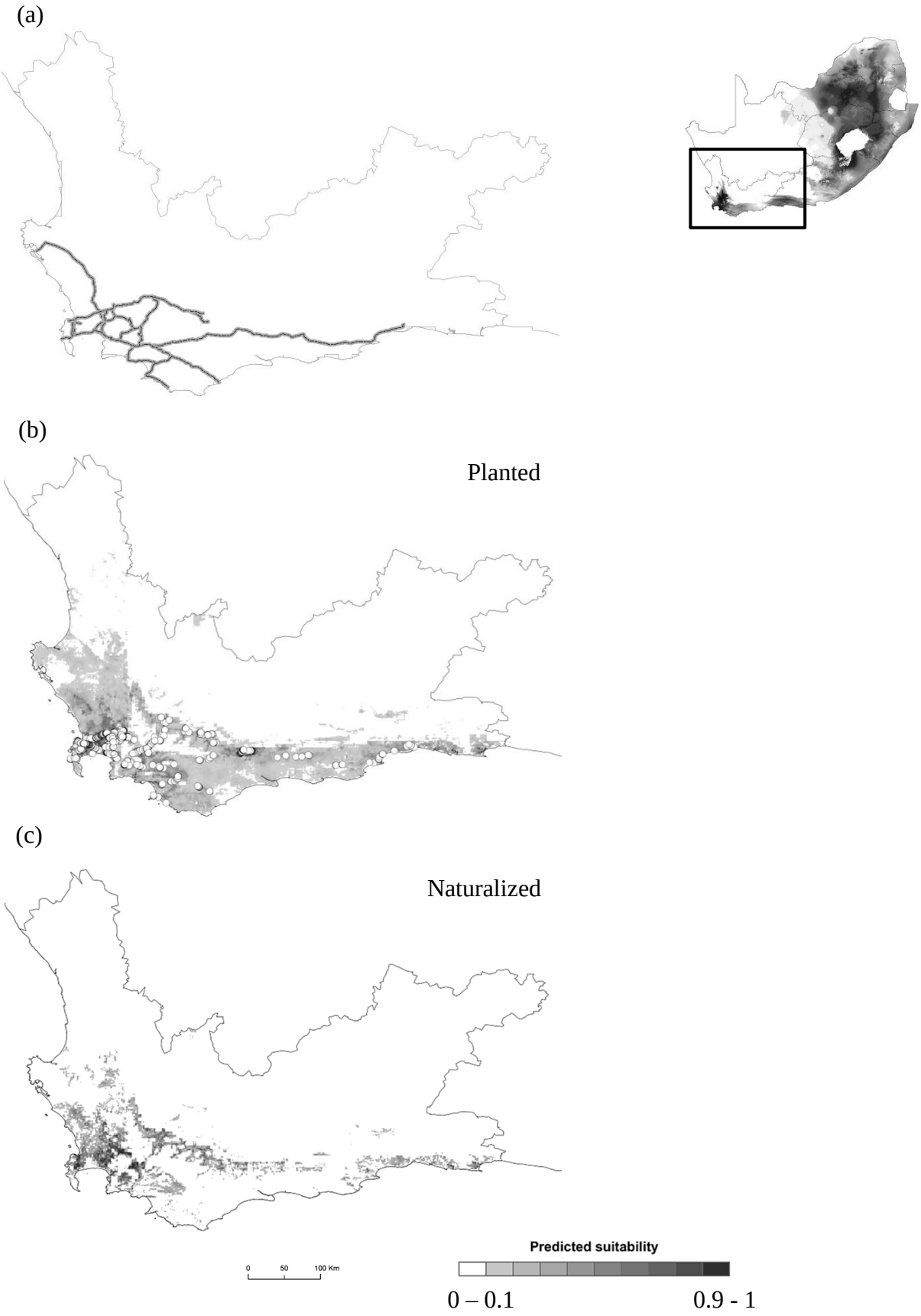


Figure 3.4.

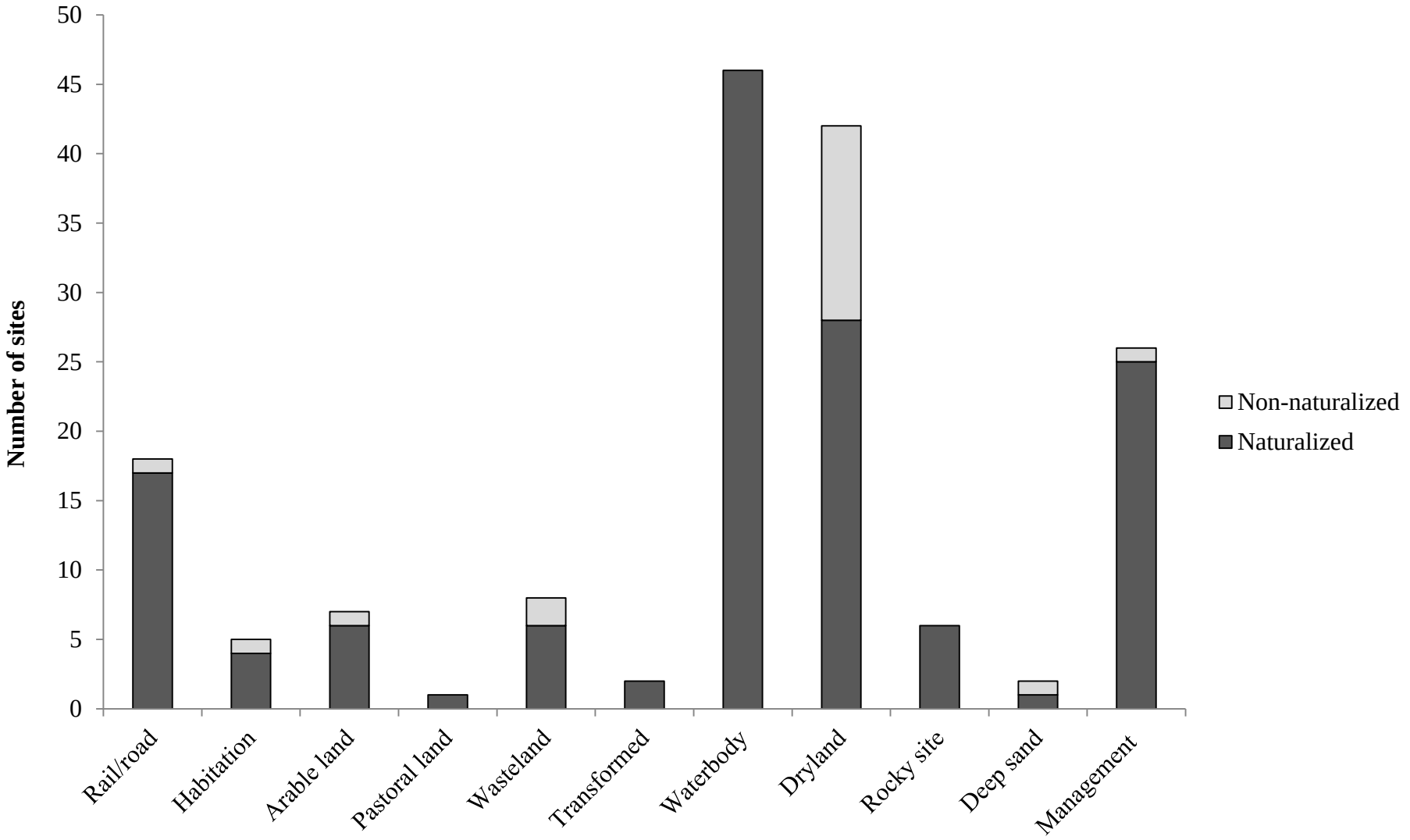

Number of sites
50
45
40
35
30
25
20
15
10
5
0
Rail/road
Habitation
Arable land
Pastoral land
Wasteland
Transformed
Waterbody
Dryland
Rocky site
Deep sand
Management
Non-naturalized
Naturalized

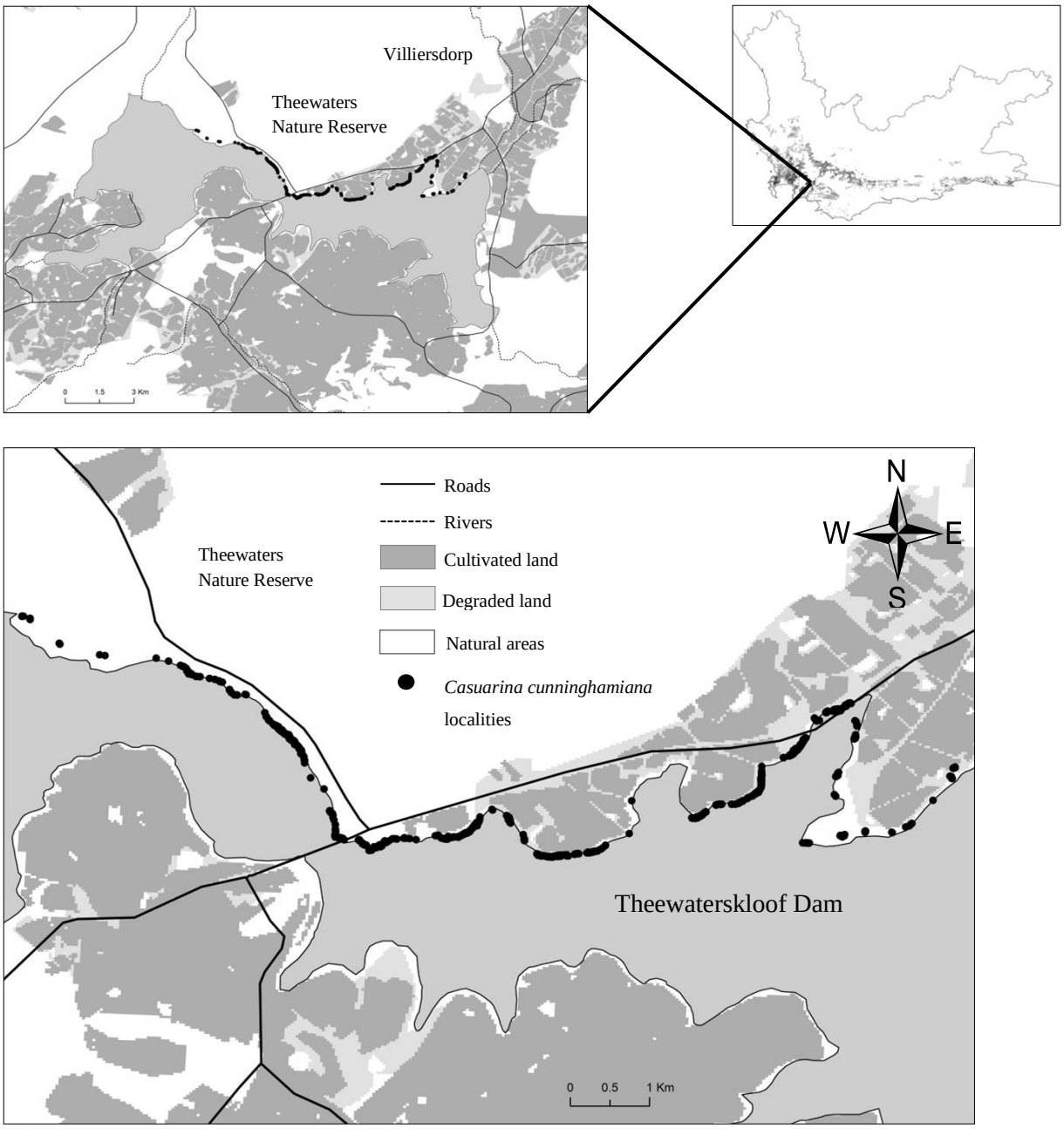
Figure 3.5.

Box 3.1. *Casuarina cunninghamiana* poses a substantial threat to vegetation around dams and reservoirs: the case of Theewaterskloof Dam, Western Cape, South Africa.

Large water bodies are particularly vulnerable to invasion by alien species and act as stepping-stones for the dispersal of these species across landscapes (Havel et al., 2005). Dams fed by surface water from agricultural and urbanized watersheds also tend to have many invasive species (Galatowitsch et al., 1999).

Established in 1978, the Theewaterskloof Dam is the largest dam in the Western Cape and has a perimeter of 82 km (Swanepoel et al., 2006). A large proportion of the land surrounding the dam is cultivated (Box 3.1. Fig. 3.1), mainly for fruit farming, where *C. cunninghamiana* is extensively planted as windbreaks. There are also several old plantations of *C. cunninghamiana* (probably established for firewood) close to the water's edge.

To obtain insight on the invasion dynamics of this species at a landscape scale, we surveyed ~20 km of the edge of the dam for both planted and naturalized individuals.



Box 3.1. Figure 3.1. Map of the Theewaterskloof Dam showing the distribution of naturalized populations of *Casuarina cunninghamiana*.

The effect of dams on seed dispersal is likely to depend on the prevailing wind speed and direction (Brown and Chenoweth, 2008). South-easterly (summer) and north-westerly (winter) winds prevail in the area. The distribution of *C. cunninghamiana* around Theewaterskloof Dam appears to be largely determined by the south-easterly wind (Box 3.1. Fig. 3.1) – most populations occur on sides of the dam exposed to wind from that direction. Naturalized individuals occur some distance from cultivated lands where *C. cunninghamiana* is planted, suggesting long-distance dispersal in water. On the cultivated land observed north-

west of the isolated naturalized populations, *Pinus radiata* was used as a windbreak, not *C. cunninghamiana*.

In its native range, *C. cunninghamiana* establishes in parts of the riparian zone that are characterised by flow variability (plants are alternately submerged and exposed) which apparently encourages growth (Roberts and Marston, 2011). The species can withstand periodic water inundation along the edge of Theewaterskloof Dam (Box 3.1. Fig. 3.2). In addition, seasonal water inundation can result in the removal of existing vegetation (Havel et al., 2005) which may open up new patches for *C. cunninghamiana* colonization.

Box 3.1. Figure 3.2. Naturalized populations of *Casuarina cunninghamiana* around the Theewaterskloof Dam, showing substantial establishment at the high-water mark. (Photos: L.J. Potgieter)

The Theewaterskloof case highlights that although most *C. cunninghamiana* spread is close to plantings, the species can spread rapidly through seed dispersal in water. The benefits (barrier trees for fruit production) occur with costs that are substantially spatially separated (several kilometres away on land managed for nature conservation).

Appendix 3.1. Species report (*Casuarina cunninghamiana* in the south-western part of the Western Cape, South Africa).

Species: *Casuarina cunninghamiana Miq.* For identification key, see Castle (2008).

Location: Western Cape, South Africa (numerous locations)

Status: Invasive; E under Blackburn et al., (2011); introduced between 1902 and 1907. Continues to be planted.

Uses: Windbreak; ornament; shade tree; firewood and charcoal; general construction purposes (poles, fences, rafters, beams, tool handles etc.) and other wood-based industries (e.g. veneer for plyboard and woodchips); soil stabilization; erosion control; intercropping; soil improvement; rehabilitation of degraded sites. The bark (rich in tannin) is used for dyeing leather and fishing nets. It is used for fodder in times of drought. The flowers are an important source of pollen for bees (U.S. National Research Council, 1984). The importance of the species for honey production in the Western Cape has yet to be recognised.

Threat: 29% of Western Cape land area at risk to invasion (possibly greater); ~1.45 M ha. Highest risk in areas within 100 m from planted individuals and water bodies or water courses.

Abundance: ~0.74 M planted trees; ~1.5 M naturalized trees in the Western Cape. At a national scale, ~2.5 M naturalized trees.

Population Growth Rate: 66% of population < 2m (8% reproductively mature).

Extent: Planted trees cover an area (minimum convex hull) of ~1.1 M ha and naturalized trees cover an area of ~0.4 M ha in the Western Cape. At a national scale, naturalized trees cover an area of ~0.6 M ha.

Spread: Seeds dispersed by wind and wate – rivers and dams likely conduits for dispersal.

Impact: Impact yet to be assessed. Established in riparian habitats - potential habitat transformer (Nel et al., 2004).

Survey method(s) used: Road surveys; each site systematically surveyed on foot at least 10 meters from any plants observed.

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References:

Blackburn, T., Pyšek, P., Bacher, S., Carlton, J., Duncan, R., et al., 2011. A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26, 333–339.

Castle, W.S., Langeland, K.A., Rockwood, D.L., 2008. *Casuarina cunninghamiana* Miq. (River sheoak) in Florida and its potential as a windbreak plant for citrus groves. *University* of *Florida's Cooperative Extension Service Publications* HS 1139.

Nel, J.L., Richardson, D.M., Rouget, M., Mgidi, T.N., Mdzeke, N., Le Maitre, D.C., van Wilgen, B.W., Schonegevel, L., Henderson, L., Neser, S., 2004. A proposed classification of invasive alien plant species in South Africa: towards prioritizing species and areas for management action. South African Journal of Science 100, 53-64.

U.S. National Research Council, 1984. Casuarinas: Nitrogen-fixing trees for adverse sites. National Academy Press, Washington D.C.

Chapter 4: *Casuarina* invasion alters primary succession on lava flows on La Réunion Island

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Contribution of each author:

LJP, JRUW, DS & DMR: Planning and discussion of the study.

LJP: Conducted all field work, statistical analyses, led the writing.

JRUW: Assisted with field work, provided comments on the manuscript and statistical advice.

DS: Assisted with field work, provided comments on the manuscript and statistical advice.

DMR: Provided comments on the manuscript and improved the writing.

Intended journal: *BIOTROPICA*

4.1 Abstract

Invasive plants can alter community dynamics and the successional trajectories of ecosystems they colonize. We explore how interactions between disturbance and invasion govern successional trajectories in the case of *Casuarina equisetifolia* invading lava flows on Réunion Island. Surveys from 1972 and 1990 were compared with results of a survey in 2012 to detail progression of the invasion over time. General additive models were used to estimate the influence of altitude, distance to putative source on introduction, and lava flow age on the abundance of *C. equisetifolia*. Based on the predictions, we estimated the likely rate and eventual extent of spread of the species in the area through time. We placed our findings in the context of a conceptual model of successional processes in the area to highlight how the invasion of *C. equisetifolia* and natural and human-mediated disturbances are changing natural vegetation dynamics. The extent of invasion by *C. equisetifolia* has increased twenty-fold over the past 40 years from 110 ha in 1972 to 2373 ha in 2012. Lava flows have facilitated this spread, and in turn *C. equisetifolia* has started to radically change successional trajectories, increasing the rate of succession sevenfold. The continued spread of this species poses a major threat to the small area of remaining native lowland rainforests on Réunion which cover < 2 % of their original extent.

Key words: Biological invasions; *Casuarina equisetifolia*; disturbance; lava flow; Réunion Island; succession; tree abundance; Mascarene Islands

Biological invasions are a growing threat to biodiversity worldwide, but are particularly problematic on oceanic islands where many ecosystems have been severely disrupted by invasive species (Mueller-Dombois *et al.* 1981, Kueffer *et al*. 2010). Biological invasions on oceanic islands provide a useful system for examining the effects of individual species on ecosystem-level phenomena (Vitousek & Walker 1989). In particular, the frequency and intensity of disturbance can facilitate invasions (Hobbs & Huenneke 1992; Davis 2003).

Volcanic eruptions, a particular dramatic disturbance, have varied and complex consequences (del Moral & Grishin 1999). In recently disturbed areas such as volcanic lava flows, some alien plant species disrupt natural plant succession at the ecosystem level (Rejmánek 1989, D'Antonio & Meyerson 2002, Titus & Tsuyuzaki 2003). Work on *Morella faya* on Hawa'ii has shown the extent to which invasive species can alter ecosystem function and benefit from natural disturbances generated by volcanic lava flows (Vitousek & Walker 1989, Lenz & Taylor 2001).

The initial establishment of invading species, as well as the timing and magnitude of peak abundance are related to the origin of propagules, phenological traits, potential for vegetative expansion, and temporal and spatial variation in disturbance (Halpern 1989). Plant invasion dynamics depend on aspects of the disturbance regime, proximity to sources of propagules, and the degree of habitat openness as well as intrinsic characteristics of the invading species and the site (Alston and Richardson 2006).

Casuarina equisetifolia is one of the most prominent invasive species in the early successional stages on volcanic lava flows on Réunion Island in the Mascerene archipelago. We aimed to: (1) evaluate the effect of key drivers (altitude, distance to source, fire and lava flow age) of the spatio-temporal abundance of *C. equisetifolia*; and (2) assess the change in successional trajectories resulting from the invasion. These insights were used to construct a conceptual model of succession in these ecosystems with and without *C. equisetifolia* as the foundation for speculation on potential future successional trajectories in remaining native lowland rainforests on Réunion.

4.2 Methods

4.2.1 Study site

Réunion Island (2512 km^2 in extent) is the least transformed of the biodiversity-rich islands of the Mascarene archipelago. Around thirty percent of the native vegetation remains intact (Strasberg *et al*. 2005), compared with less than five percent for Mauritius and none for Rodrigues (Cheke & Hume 2008, Thébaud *et al*. 2009). However, Réunion's ecosystems face many threats, including severe and rapidly escalating impacts due to invasive alien species, especially plants (Lavergne *et al*. 1999; Baret *et al*. 2004, 2006).

The study site was situated on the lower slopes of the Piton de la Fournaise volcano in the south-east of Réunion Island (Fig. 4.1). This volcano formed around 500 000 yrs ago on the flanks of the now extinct Piton des Neiges volcano. The lava flows of the Piton de la Fournaise volcano have an unusual spatial distribution: ninety-five percent of those occurring in the last 300 yrs are located in a U-shaped caldera (an area named the Grand Brûlé) opening to the east towards the Indian Ocean (Fig. 4.1). Piton de la Fournaise has erupted once every nine months over the last century (Michon *et al*. 2013).

The system has been well studied and mapped and it is possible to distinguish different lava flows from 1900 onwards. The frequency of lava flows and the spatial dynamics of plant succession have resulted in a matrix of different-aged vegetation communities, with pockets of natural lowland rainforest persisting in matrix of different aged lava flows (Litrico *et al.* 2005). The area has also been subjected to human-induced disturbances (*e.g.* a fire in 1993 swept through most of the lower reaches of the caldera, see Fig. 4.1).

4.2.2 Study species

Casuarina equisetifolia (Casuarinaceae) is an evergreen tree native to Australia, Southeast Asia and the Pacific archipelagos (Morton 1980). It typically grows to a height of 20-30 m and has been widely planted in many parts of the world for agroforestry, erosion control, intercropping, shelter and windbreaks, and has become invasive on four continents (Rejmánek & Richardson 2013; Potgieter *et al*. 2014). It is also invasive on many islands including Ascension, Bermuda, Canary Islands, Cayman Islands, Dominican Republic, Hawaii, Jamaica, Ogasawara, Puerto

Rico, Seychelles (Kueffer *et al*. 2010). The species has a range of traits that enhance its invasive capacity and ability to cause impacts in invaded ecosystems, including rapid growth; tolerance of high salinity, cold temperatures, low soil fertility and arid conditions; the capacity to establish and propagate easily; the ability to coppice (Potgieter *et al*. 2014). Symbiotic associations with N-fixing actinobacteria from the genus *Frankia* as well as ecto-, endo- and arbuscular mycorrhizal fungi allow *C. equisetifolia* to grow on extremely nutrient-poor substrates (Zhong *et al*. 1995, Diagne *et al*. 2013).

Casuarina equisetifolia was introduced to La Réunion in 1768, primarily as a source of firewood and erosion control (Kueffer & Vos 2004) and has become a prominent invader (Baret *et al.* 2006). By the early 1900s, most fuel-wood used in the lowlands came from *C. equisetifolia* plantations along the coast (Cheke & Hume 2008). After World War II, the Forest Service initiated a large-scale planting programme to replace natural forest with alien species of *Acacia*, *Casuarina* and *Cryptomeria* (Kueffer & Lavergne 2004). Low-altitude habitats were greatly reduced, transformed and fragmented through a combination of human activities (agriculture and urbanization) and invasion by introduced species (Strasberg *et al*. 2005).

Casuarina equisetifolia is a major transformer species on the island, forming dense monospecific stands that affect nutrient cycling (Kueffer & Lavergne 2004). It is the most prominent invasive species on volcanic lava flows on La Réunion Island, and invasive stands are known to disrupt primary succession (Macdonald *et al.* 1991).

4.2.3 Survey methods

We collated all data on the abundance and height of *C. equisetifolia* from two previous censuses in 1972 (Cadet 1977) and in 1990 (D. Strasberg & J. Lepart unpubl. data., Strasberg 1994) and undertook detailed field surveys in 2012-2013 repeating the sampling protocol.

A total of 102 temporary plots (10 m x 10 m in size with 3 replicates per lava flow) were established in the Grand Brûlé area on lava flows of different ages at different altitudes. Wherever possible, plots were established at the same location as plots from the previous surveys. In locations that were inaccessible due to impenetrable vegetation, plots were established as close as possible to previous sampling sites on the same lava flow. An additional

22 plots were established outside the caldera to the south where lava flows are infrequent and fire has yet to occur. The number of *C. equisetifolia* individuals in each plot was counted and the height of each individual was estimated.

To determine to the location of the initial seed source, we obtained historic records of the first known occurrence of *C. equisetifolia* in the Grand Brûlé area. To measure the proximity of each plot from all three surveys to this initial source, we used the 'Near' tool from the 'Proximity Analysis' toolbox in ArcMap.

In addition, ten altitudinal density transects were conducted on lava flows of different ages. This was done by walking up each recent lava flow with a handheld Global Positioning System (Garmin GARMAP 62S) and marking waypoints of every individual *C. equisetifolia* plant within 20 m from the edge of the older adjacent lava flow.

4.2.4 Data analysis

Because the ages of substrates are known, side-by-side flows differing in age can be compared (*e.g.* Drake & Mueller-Dombois 1993) and ecosystem properties can be studied on individual flows that extend across broad altitudinal gradients (*e.g.* Vitousek *et al*. 1992, Aplet & Vitousek 1994).

Preliminary analyses showed the relationships of tree abundance and height, with altitude, distance to source and lava age to be non-linear. We combined Generalised Additive Models (GAMs, Hasti & Tibshirani 1990) to evaluate the effect of these variables on the abundance and size of *C. equisetifolia* trees. This was done for datasets from three surveys: those conducted by T. Cadet in 1972 (Cadet 1977), D. Strasberg & J. Lepart in 1990 (unpubl. data), and this study.

We used the default parameters for the GAM as outlined in the R Statistical package, version 3.0.0 (R Development Core Team 2010) with the 'gam' library. AIC (Akaike Information Criteria) with forward stepwise selection was used, where the lowest AIC value for every possible combination of explanatory variables was chosen, starting with the explanatory variable with the best fit. Model performance was evaluated by an analysis of deviance.

We combined results from the GAMS with historical evidence to develop a conceptual model comparing natural and invaded successional processes in light of natural and human-mediated disturbances.

4.2.5 Mapping

Aerial photos obtained from Réunion National Park, historic topographical maps, and maps obtained from the Geology Department at Réunion University were used to reconstruct the history of disturbances (lava flows and fire) in the Grand Brûlé area (Fig. 4.1).

Altitudinal bands were calculated using a 20-m resolution digital elevation model (DEM) using the Spatial Analyst extension of ArcGIS. The surface areas of each 20-m band were calculated using the raster-based method of Jenness (2004). The areas of the altitudinal bands were used to estimate abundance over the study site for all three surveys, based on the GAM models. These predictions were generated using the 'predict.gam' function in R.

We developed a predictive surface of *C. equisetifolia* occurrence across the study site in ArcGIS 10.0. Because the GAM does not yield parameter coefficients, we could not simply use map algebra to create a predictive surface. Rather, we created a lattice of data points separated by 20 m using the ArcGIS extension ET Geo Wizards 9.9 (Tchoukanski 2009). The variable grid-cell values were then exported from ArcMAP and used in the GAMs to generate predicted probabilities of tree occurrence. The predicted values were returned to ArcMap for plotting. We used the Geostatistical Analyst extension to create an inverse distance-weighted interpolation based upon the imported logistic values. The final output was a predictive surface (expressed as percentage ground cover) of the study site based upon the best statistical model.

4.3 Results

4.3.1 Spatio-temporal changes of *Casuarina* range, abundance and cover on lava flows

The area covered by *C. equisetifolia* has increased significantly over time (Fig. 4.2). In 1972, *C. equisetifolia* covered around 110 ha (5%) of the caldera and was strictly confined to areas along the coast. By 1990, *C. equisetifolia* had spread to higher altitudes and the area covered increased

to 1436 ha (15%) and then to 2373 ha (24%) by 2012. *Casuarina equisetifolia* had become more widespread, occurring at high densities along the coast (Fig. 4.2b, c).

High abundance is observed on younger lava flows at lower altitudes (Fig. 4.4). Strasberg & Lepart in 1990 and Potgieter *et al*. in 2012 observed high densities at low altitudes, with few individuals occurring between 300 and 350 m and no trees occurring over 400 m. Recruitment is significantly higher on more recent lava flows (Fig. S4.3c).

4.3.2 Rate of spread

Figure 4.2 shows the upper altitudinal limits for *C. equisetifolia* over time. In 1972, trees were confined to altitudes lower than 100 m (Fig. 4.2a), but by 1990, invasive populations extend up to 350 m in altitude (Fig. 4.2b). The same altitudinal limit was observed in 2012 (Fig. 4.2c), suggesting that upward movement might only happen if climate were to change.

From 1972 to 1990, *C. equisetifolia* spread at a rate of 69 ha/yr. By 2012, *C. equisetifolia* had become even more widespread – reflecting a spread rate of 45 ha/yr. Therefore, at the current frequency of lava flows, by the year 2050, *C. equisetifolia* will have spread a further 1710 ha, occupying (at varying densities) over 4000 ha.

4.3.3 Tree size

The tallest trees are found on lava flows older than 60 yrs (Fig. S4.4, Fig. 4.5) while smaller trees are found on younger lava flows. Tree height decreases at higher altitudes. A significant difference (Fig. S4.5, t-test, $P < 0.05$) was found between the number of juvenile trees (< 4 m) on younger lava flows (< 25 yrs old) and that on older lava flows (> 25 yrs old). Therefore, recruitment on older lava flows with well-established *C. equisetifolia* trees (and other alien vegetation) is lower than that on younger lava flows.

4.3.4 Alteration of successional trajectories

The ingress of *C. equisetifolia* has increased the rate of primary succession (sensu Walker & Moral 2003) on new lava flows sevenfold, thus disrupting natural plant succession processes (Fig. 4.5). The time taken to reach canopy closure differs significantly between invaded and non-

invaded systems (chi-square = 57.1; P < 0.001). Disturbances have played a role in augmenting natural succession on these lava flows (Fig. S4.6).

4.4 Discussion

The extent of the *Casuarina equisetifolia* invasion has increased dramatically over the past few decades, with the disruption caused by new lava flows a major factor in facilitating this spread. Here we discuss how this invasion is likely to have radically changed successional trajectories.

We predict that at most, 30 % of the caldera will be invaded as a) there is a limit to how quickly *C. equisetifolia* will colonise new lava (first plants appear after 8 – 15 yrs, reaching canopy closure by around 60 yrs); and b) *C. equisetifolia* appears to be limited to lower altitudes (below 400 m, Fig. 4.3a). The altitudinal limit was also evident on a 27 year-old lava flow situated outside the caldera (Fig. 4.3b), although densities declined at lower altitudes (< 300 m).

Disturbances may create dispersal corridors, facilitating invasion by removing competition and forming open areas for dispersing propagules (Hobbs & Huenneke 1992). A comparison between Figures 4.3a and b show how *C. equisetifolia* is strictly confined to lower altitudes in the absence of disturbance, suggesting that lava flows have allowed for the spread of *C. equisetifolia* to higher altitudes.

4.4.1 Primary succession on the Grand Brûlé lava flows

Primary succession is the process of ecosystem development on barren surfaces where severe disturbances have removed most vestiges of biological activity (Walker & Moral 2003). The rate of primary succession in native lowland rainforests on Grand Brûlé lava flows is influenced by climate, the moisture-holding and nutrient status of the substrate, the accessibility of the site to pioneer plants, interactions among pioneers on the site, and modification of the site by the pioneers (Drake & Mueller-Dombois 1993). Contrary to conventional models of succession, where herbaceous plant species first colonise, followed by the late arrival of woody plants (*e.g.* Sastre & Fiard 1986), the early stages of succession on Grand Brûlé lava flows are dominated by woody plants. All colonising plants are recruited from seed rain from surrounding areas. Colonisation rates are significantly higher for wind-dispersed species than for vertebrate-dispersed trees (Thébaud & Strasberg 1997); the difference between dispersal modes is more

pronounced on younger lava flows. The rapid colonisation by wind-dispersed woody species on Grand Brûlé is similar to that on Hawaiian lava flows which have similar climatic and substrate conditions (Chevènement 1990, Aplet & Vitousek 1994). The density of these native wind-dispersed species rapidly decreases on older lava flows while bird-dispersed trees and shrubs arrive late in the succession increase in richness and abundance as the substrate ages (Rivals 1952, Cadet 1977, Strasberg 1994). Nevertheless, Thébaud & Strasberg (1997) reported very low colonisation rates of most native fleshy-fruited trees from the forest edges to surrounding lava flows (< 0.1 m/yr). They observed a negative correlation between fruit size and colonisation rate and suggested that the low dispersal capacity of late-successional trees is due to the recent extinction of large frugivores on the island.

4.4.1.1 Early succession altered by *Casuarina equisetifolia* invasion

Along altitudinal gradients factors such as propagule pressure, climatic conditions and biotic interactions change simultaneously across over short distances (Alexander *et al*. 2009). Poll *et al*. (2009) demonstrated that over altitudinal gradients, abiotic conditions need not be important constraints for the recruitment phase of an invasion by an alien plant. More important is the extent to which altitude is a proxy for the level of seed rain – in this case whether propagules reach higher altitudes. Strasberg (1994) showed that pioneer communities on the Grand Brûlé lava flows are primarily structured according to altitude, and secondarily according to substrate age. Alien tree species that were dominant at low altitudes decreased in abundance with an increase in altitude. Our results support this finding. An upper altitudinal limit exists for *C. equisetifolia*, as shown by the decrease in abundance at higher altitudes (Fig. 4.2, Fig. S4.2). Low abundances were observed on older lava flows (> 1801 yrs) at high altitudes (Fig. 4.4a). This may be explained by the short residence time of *C. equisetifolia* (introduced in 1768), as the initial putative source is near the coast. Furthermore, in the absence of lava flows (disturbance), *C. equisetifolia* is likely to be increasingly limited at high altitudes by dispersal constraints (low propagule pressure) and high climatic and biotic resistance (*e.g.* competition with pre-established vegetation). The slow progression of *C. equisetifolia* upwards over time likely coincides with the frequency of lava flows. Tree height was also found to decrease at higher altitudes (Fig. S4.4). These results are consistent with observations that trees become stunted and have more open

canopies at high altitudes (Coomes & Allen 2007). The decline in tree height with altitude may be explained by reduced air and soil temperatures and/or increased precipitation.

4.4.1.2 Late succession altered by bird-dispersed invasive trees

The relative abundance and diversity of alien species is low in the early successional stages on Grand Brûlé, but increases on older flows. This is probably due to the harsher conditions experienced during early successional stages (Macdonald *et al.* 1991) or because early-successional species are predominantly wind-dispersed natives, whereas late-successional species are bird-dispersed alien species (Strasberg 1996). Small fleshy-fruited species colonizing lava flows are mainly shade-tolerant alien plants (such as *Psidium cattleianum*) that have a clumped distribution, with a high concentration of young trees and shrubs beneath well-established wind-dispersed species such as *Agarista salicifolia* and, increasingly, *C. equisetifolia* (Strasberg 1994, 1995). Invasive fleshy-fruited trees disrupt long-term forest succession processes. From surveys in 1989, Macdonald *et al.* (1991) suggested that native species are unlikely to assume dominance on lava flows younger than 100 yrs unless active management of alien species is undertaken.

4.4.2 The role of fire in facilitating *Casuarina equisetifolia* invasions

The 1993 fire which burned across most of Grand Brûlé may account for the decrease in *C. equisetifolia* density by 2012. Testing the effect of the fire on *C. equisetifolia* population dynamics is problematic as young lava flows (< 200 yrs) were disproportionally well sampled due to ease of access. Dense *C. equisetifolia* forests have established on lava flows older than 200 yrs in the centre Grand Brûlé since the fire in 1993 (pers. observ.).

Casuarina equisetifolia is susceptible to fire (Boland *et al*. 1984, U.S. National Research Council 1984, Rockwood & Geary 1991, Parrotta 1993), but it has been noted to recover partially after fire by resprouting from basal roots (Smith 1998). Fire removes much of the plant canopy and has a short-term fertilizing effect on the soil - both light and nutrient availability can be increased temporarily (Kauffman 1990, Hobbs & Huenneke 1992). This may create conditions suitable for *C. equisetifolia* establishment.

4.4.3 The fate of *Casuarina equisetifolia* on Réunion Island

Forests of *C. equisetifolia* have existed on Grand Brûlé for over a century, and their abundance and influence on the native vegetation and on successional patterns is constantly changing. To provide guidelines for management of the shrinking lowland forests on La Réunion, we need to predict how processes will change in the future. Here we expand on key aspects of the conceptualization presented in Fig. 4.5.

Shade tolerance is essential for invasions of forests by alien plants, and largely determines long-term invasion abundance (Martin *et al*. 2010). *Casuarina equisetifolia* is a shade-sensitive species (U.S. National Research Council 1984). Dense populations of shade-intolerant trees typically self-thin following canopy closure (Drake & Mueller-Dombois 1993). The typically shade-intolerant species of pioneer vegetation tend to be replaced by shade-tolerant trees as succession proceeds (Drake & Mueller-Dombois 1993).

We have shown recruitment on older lava flows with well-established *C. equisetifolia* trees (and other alien vegetation) to be lower in comparison to younger lava flows, suggesting that recruitment is episodic. Therefore, the rate of spread of *C. equisetifolia* may be lower in the absence of lava flows. Lava flows may serve as an effective dispersal pathway for this species. These findings also suggest that on older substrates, self-thinning of *C. equisetifolia* has already begun. These findings support the notion that lava flows facilitate the spread of *C. equisetifolia*. With unremitting lava flow formation, and continued presence of *C. equisetifolia* in the ecosystem, we can expect this species to persist and expand unless intensive removal plans are implemented.

As seen on the Hawaiian Islands, once *C. equisetifolia* is established, forests of this species are not easily colonized by native species (Mascaro *et al*. 2008), although we cannot discount the possibility that continued succession will lead to a greater abundance of native species. However, because native forests are undergoing succession toward dominance by alien tree species, it seems unlikely that increased forest age will encourage substantial recovery of native species.

The impacts of *C. equisetifolia* on ecosystem functioning have not be studied, but seem to be similar in nature and magnitude to those reported for *Morella faya* on the Hawai'i islands

(Vitousek & Walker 1989). It will be very difficult and expensive to return this ecosystem to its previous state, and careful consideration needs to be given to developing appropriate management goals and approaches to either achieve whatever level of "remediation" is practical, or to manage the *C. equisetifolia*-dominated ecosystem to achieve particular goals.

4.4.4 Options for management

Control efforts need to be concentrated in areas that are considered the most intact, and representative of the diversity found within the island. Management must consider not only alterations of the original disturbance regime, but also alteration in the pool of potential responding species. The management approach should include research and monitoring following these actions.

Preventing further spread and reducing the density of *C. equisetifolia* by mechanically removing trees and seedlings and applying herbicides may ultimately prove to be futile. In the case of *Morella faya* on Hawai'i Volcanoes National Park, Lenz & Taylor (2001) explain how expensive control methods had limited success.

In 2007, Réunion Island Forestry Service initiated a control programme for *C. equisetifolia* along the south-eastern coast (supralittoral zone) with the aim of restoring coastal habitat. Results have been promising at local scales, with native species reintroduction in small pockets less than 0.5 ha. A national invasive species committee has been set up and on-going research projects attempt to assess the impacts of control methods. Problem species and areas have to be prioritised for control.

Casuarina equisetifolia may be an excellent candidate for biological control because of its large native range, number of congeners, and known enemies (Pemberton 1996). However, work on biocontrol has been hampered by perceived conflicts of interest.

4.5 Conclusions

Volcanic landscapes provide valuable insights into fundamental ecological processes. This study has demonstrated how a single invasion of *C. equisetifolia* can have a major effect on successional development to transform a landscape. The degree to which *C. equisetifolia*

continues to spread across the lowland regions of Réunion Island will, to a large extent, determine the fate of the unique native lowland rainforests.

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References

AINSWORTH, A. AND J. B. KAUFFMAN. 2010. Interactions of fire and nonnative species across an elevation/plant community gradient in Hawai'i Volcanoes National Park. Biotropica, 42: 647–655.

ALLISON, S. D. AND P. M. VITOUSEK. 2004. Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. Oecologia 141: 612–619.

ALSTON, K. P., AND D. M. RICHARDSON. 2006. The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. Biol. Conserv. 132: 183–198.

APLET, G. H. AND P. M. VITOUSEK. 1994. An age-altitude matrix analysis of Hawaiian rain-forest succession. J. Ecol. 82: 137-147.

APLET, G. H. 1990. Alteration of earthworm community biomass by the alien *Myrica faya* in Hawai'i. Oecologia 92: 414–416.

ATKINSON, I. A. E. AND E. W. CAMERON. 1993. Human influence on the terrestrial biota and biotic communities of New Zealand. Trends Ecol. Evol. 8: 447–451.

BACHELERY, P. 1981. Le Piton de la Fournaise (Ile de La Réunion), Etude volcanologique, structural et pétrologique. PhD Dissertation, Université de Clermont-Farrand, France.

BARCELO, A. AND J. COUDRAY. 1996. New annual isohyet and rainfall maxima map for the Piton de la Fournaise massif (Réunion Island). Revue des sciences de l'*eau* 4: 457-484.

BARET, S., S. MAURICE, T. LE BOURGEOIS, AND D. STRASBERG. 2004. Altitudinal variation in fertility and vegetative growth in the invasive plant *Rubus alceifolius* Poiret (Rosaceae), on Réunion Island. Plant Ecol. 172: 265–73.

BARET, S., M. ROUGET, D. M. RICHARDSON, C. LAVERGNE, B. EGOH, J. DUPONT, AND D. STRASBERG. 2006. Current distribution and potential extent of the most invasive alien plant species on La Réunion (Indian Ocean, Mascarene Islands). Austral Ecol. 31: 747-758.

BARUCH, Z. AND G. GOLDSTEIN. 1999. Leaf construction cost, nutrient concentration, and net CO_2 assimilation of native and invasive species in Hawai'i. Oecologia 121: 183-192.

BOLAND, D. J., M. I. H. BROOKER, G. M. CHIPPENDALE, N. HALL, B. P. M. HYLAND, R. D. JOHNSTON, D. A. KLEINIG, AND J. D. TURNER. 1984. Forest Trees of Australia. CSIRO Nelson, Melbourne, Victoria.

BUCKLEY, Y. M., B. M. BOLKER, AND M. REES. 2007. Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. Ecol. Lett. 10: 809-817.

CADET, T. 1977. La végétation de l'ile de La Réunion: Étude phytoécologique et phytosociologique. PhD Dissertation, Université d'Aix-Marseille, France.

CARINO, D. A., AND C. C. DAEHLER. 2002. Can inconspicuous legumes facilitate non-native grass invasions? Partridge peas and fountain grass in Hawai'i. Ecography 25: 33–41.

CHEKE, A., AND J. HUME. 2008. Lost land of the Dodo: an ecological history of the Mascarene Islands. T and AD Poyser, London.

CHEVENNEMENT, R. 1990. La colonisation végétale d'un champs de lave de La Réunion. Compte-rendu sommaire des Séances de la Société de biogéographie 66: 47-63.

CHRISTENSEN, P. E., AND N. D. BURROWS. 1986. Fire: an old tool with a new use. *In* R. H. Groves, and J. J. Burdon (Eds.). Ecology of biological invasions: an Australian perspective, pp. 57-66. Australian Academy of Science, Canberra, Australia.

COOMES, D. A., AND R. B. ALLEN. 2007. Effects of size, competition and altitude on tree growth. J. Ecol. 95: 1084-1097.

CORDELL, S., G. GOLDSTEIN, D. MUELLER-DOMBOIS, D. WEBB, AND P. M. VITOUSEK. 1998. Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawai'ian tree species, along an altitudinal gradient: the role of phenotypic plasticity. Oecologia 113: 188-196.

CRAWLEY, M. J. 1993. GLIM for ecologists. Blackwell Scientific Publications, Oxford.

D'ANTONIO, C. M., AND T. L. DUDLEY. 1995. Biological invasions as agents of change on islands versus mainlands. *In* P. M. Vitousek, L. L. Loope, and H. Adsersen (Eds.).

Islands: biological diversity and ecosystem function, pp. 103–121. Springer Verlag, Berlin, Germany.

D'ANTONIO, C. M., AND L. A. MEYERSON. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restor. Ecol. 10: 703–713.

DAVIS, M. A. 2003. Biotic globalization: does competition from introduced species threaten biodiversity? BioScience 53: 481–489.

DAVIS, M. A., J. P. GRIME, AND K. THOMPSON. 2000. Fluctuating resources in plant communities: A general theory of invasibility. J. Ecol. 88: 528–534.

DEL MORAL, R., AND S. Y. GRISHIN. 1999. Volcanic disturbances and ecosystem recovery. *In* L. R. Walker (Ed.). Ecosystems of disturbed ground, pp. 137-160. Elsevier, New York, USA.

DENSLOW, J. S., J. C. SPACE, AND P. A. THOMAS. 2009. Invasive exotic plants in the tropical pacific islands: patterns of diversity. Biotropica 41: 162–170.

DIAGNE N, D. DIOUF, S. SVISTOONOFF, A. KANE, K. NOBA, C. FRANCHE, D. BOGUSZ, AND R. DUPONNOIS. 2013. *Casuarina* in Africa: Distribution, role and importance of arbuscular mycorrhizal, ectomycorrhizal fungi and *Frankia* on plant development. J Environ. Manage. 128: 204-209.

DRAKE, D. R., AND D. MUELLER-DOMBOIS. 1993. Population development of rain forest trees on a chronosequence of Hawaiian lava flows. Ecology 74: 1012-1019.

ELFERS, S. C. 1988. Element Stewardship Abstract for *Casuarina equisetifolia*. Report to The Nature Conservancy, 14 p. On file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Fire Sciences Laboratory, Missoula.

ESRI. 2010. ArcGIS Desktop. Redlands, CA, USA.

GERRISH, G., AND D. MUELLER-DOMBOIS. 1980. Behavior of native and non-native plants in two tropical rain forests on Oahu, Hawai'ian Islands. Phytocoenologia 8: 237–295.

GRUBB, P. J. 1986. The ecology of establishment. *In* A. D. Bradshaw, D. A. Goode, and E. Thorp (Eds.). Ecology and design in landscape, pp. 83-97. Blackwell Scientific Publications, Oxford.

GRUBB, P. J. 1987. Some generalizing ideas about colonization and succession in green plants and fungi. *In* A. J. Gray, M. J. Crawley, and P. J. Edwards (Eds.). Colonization, succession and stability, pp. 81-102. Blackwell Scientific Publications, Oxford.

HADDAD, N. M., J. HAARSTAD, AND D. TILMAN. 2000. The effects of long-term nitrogen loading on grassland insect communities. Oecologia 124: 73–84.

HALPERN, C. B, P. M. FRENZEN, J. E. MEANS, AND J. F. FRANKLIN. 1990. Plant Succession in Areas of Scorched and Blown-Down Forest after the 1980 Eruption of Mount St. Helens, Washington. J. Veg. Sci. 1: 181-194.

HALPERN, C. B. 1989. Early successional patterns of forest species: Interactions of life history traits and disturbance. Ecology 70: 704-720.

HAMMERTON, J. 2001. Casuarinas in the Bahamas: a clear and present danger. Bahamas J. Sci. 9: 2–14.

HASTI, T., AND R. TIBSHIRANI, 1990. Generalized additive models. Chapman and Hall, New York.

HOBBS, R. J., AND L. F. HUENNEKE. 1992. Disturbance, diversity, and invasion: implications for conservation. Conserv. Biol. 6: 324–337.

HUGHES, F., AND J. S. DENSLOW. 2005. Invasion by a N_2-fixing tree alters function and structure in wet lowland forests of Hawai'i. Ecol. Appl. 15: 1615–1628.

HULME, P. E. 2004. Invasions, islands and impacts: a Mediterranean perspective. *In* J. M. Fernandez-Palacios, and C. Morici (Eds.). Island ecology, pp. 359–383. Asociación Española de Ecología Terrestre, Madrid.

HUTTLE, C. 1992. Vegetacion en coladas de lava. Vol. 1 ORSTOM, Fundacion Charles Darwin par alas islas Galapagos, Quito.

JENNESS, J. S. 2004. Calculating landscape surface area from digital elevation models. Wildlife Soc. B. 32: 829–839.

KAUFFMAN, J. B. 1990. Ecological relationships of vegetation and fire in Pacific northwest forests. *In* J. D. Walstad, S. Radosevich, and D.V. Sandberg (Eds.). Natural and prescribed fire in the Pacific Northwest Forests, pp. 39-52. Oregon State University Press, Corvallis, Oregon.

KUEFFER, C., AND C. LAVERGNE. 2004. Case Studies on the Status of invasive Woody Plant Species in the Western Indian Ocean. 4. Réunion. Forest Health and Biosecurity Working Papers FBS/4-4E. Forestry Department, Food and Agriculture Organization of the United Nations, Rome, Italy.

KUEFFER, C., AND P. VOS. 2004. Case studies on the status of invasive woody plant species in the western Indian Ocean: 5. Seychelles. Forestry Department, FAO, UN.

KUEFFER, C., C. C. DAEHLER, C. W. TORRES-SANTANA, C. LAVERGNE, J.-Y. MEYER, R. OTTO, AND L. SILVA. 2010. A global comparison of plant invasions on oceanic islands. Perspect. Plant Ecol. Evol. Syst. 12: 145–161.

LAVERGNE, C., J. RAMEAU, AND J. FIGIER. 1999. The invasive woody weed *Ligustrum robustum* subsp. *walkeri* threatens native forests on La Réunion. Biol. Invasions 1: 377–392.

LENZ, L., AND J. A. TAYLOR. 2001. The influence of an invasive tree species (*Myrica faya*) on the abundance of a non-native insect (*Sophonia rufofascia*) in Hawai'i Volcanoes National Park. Biol. Conserv. 102: 301–307.

LITRICO, I., J. RONFORT, R. VERLAQUE, AND J. D. THOMPSON. 2005. Spatial structure of genetic variation and primary succession in the pioneer tree species *Antirhea borbonica* on La Réunion. Mol. Ecol. 14: 1575-1584.

LOCKWOOD, J. P., P. W. LIPMAN, L. D. PETERSON, AND F. R. WARSHAUER. 1988. Generalized ages of surface lava flows of Mauna Loa Volcano, Hawai'i. U.S. Geological Survey Miscellaneous Publications Map I-1908, US Government Printing Office, Washington, DC.

LONSDALE, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522–1536.

LOOPE, L. L., AND D. MUELLER-DOMBOIS. 1989. Characteristics of invaded islands, with special reference to Hawaii. *In* J. A. Drake, H. A. Mooney, F. Di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson (Eds.). Biological invasions: A global perspective, pp. 257–281. John Wiley and Sons, Chichester.

LUGO, A. E. 2004. The outcome of non-native tree invasions in Puerto Rico. Front. Ecol. Environ. 2: 265–273.

MACDONALD, I. A. W., AND J. COOPER. 1995. Insular lessons for global biodiversity conservation with particular reference to alien invasions. *In* P. M. Vitousek, L. L. Loope, and H. Andersen (Eds.). Islands: biological diversity and ecosystem function, pp. 189–204. Springer-Verlag, Berlin.

MACDONALD, I. A. W., C. THÉBAUD, W. A. STRAHM, AND D. STRASBERG. 1991. Effects of alien plant invasions on native vegetation remnants on La Réunion (Mascarene Islands, Indian Ocean). Environ. Conserv. 18: 51–61.

MACK, M., AND C. M. D'ANTONIO. 1998. Impacts of biological invasions on disturbance regimes. Trends Ecol. Evol. 13: 195–198.

MACK, R. N., AND W. M. LONSDALE. 2002. Eradicating invasive plants: Hard-won lessons from islands. *In* C. R. Veitch, and M. N. Clout Turning the tide: The eradication of invasive species, pp. 164–172. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland.

MARTIN, P. H., C. D. CANHAM, AND R. K. KOBE. 2010. Divergence from the growth–survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. J. Ecol. 98: 778–789.

MASCARO, J., K. K. BECKLUND, R. F. HUGHES, AND S. A. SCHNITZER. 2008. Limited native plant regeneration in novel, non-native-dominated forests on Hawai'i. Forest Ecol. Manag. 256: 593–606.

MICHON, L., A. DI MURO, N. VILLENEUVE, C. SAINT-MARC, P. FADDA, AND F. MANTA. 2013. Explosive activity of the summit cone of Piton de la Fournaise volcano (La Réunion island): A historical and geological review. J. Volcanol. Geoth. Res. 263: 117–133.

MORTON, J. F. 1980 The Australian pine or beefwood (*Casuarina equisetifolia* L.) an invasive ‘‘weed’’ tree in Florida. Proceedings of the *Florida State Horticultural Society* 93: 87–95.

MOULTON, M. P., AND S. L. PIMM. 1986. Species introductions to Hawaii. *In* H. A. Mooney, and J. A. Drake (Eds.). Ecology of biological invasions of North America and Hawaii, pp. 231–249. Springer, New York.

MUELLER-DOMBOIS, D. 1992. Distributional dynamics in the Hawaiian vegetation. Pac. Sci. 46: 221-231.

MUELLER-DOMBOIS, D. 2001. Biological invasion and fire in tropical biomes. *In* K. E. M. Galley, and T. P. Wilson (Eds.). Proceedings of the Invasive Species Workshop: the role of fire in the control and spread of invasive species. Fire conference 2000: the first national congress on fire ecology, prevention, and management, pp. 112-121. Miscellaneous Publication Number 11. Tall Timbers Research Station, Tallahassee, Florida, USA.

MUELLER-DOMBOIS, D., K. W. BRIDGES, AND H. L. CARSON, (Eds). 1981. Island ecosystems: Biological organization in selected Hawaiian communities. Hutchinson Ross, Stroudsburg, PA.

OSTERTAG, R., AND J. H. VERVILLE. 2002. Fertilization with nitrogen and phosphorus increases abundance of non-native species in Hawai’ian montane forests. Plant Ecol. 162: 77–90.

PARROTTA, J. A. 1993. *Casuarina equisetifolia* L. ex J. R. & G. Forst. *Casuarina*, Australian pine. Research notes, New Orleans: USDA Forest Service, Southern Forest Experiment Station, pp. 11-14.

PEMBERTON, R. W. 1996. The potential of biological control for the suppression of invasive weeds of southern environments. Castanea 61: 313-319.

PLATT, W. J., AND J. H. CONNELL. 2003. Natural disturbances and directional replacement of species. Ecol. Monogr. 73: 507-522.

POLL, M., B. J. NAYLOR, J. M. ALEXANDER, P. J. EDWARDS, AND H. DIETZ. 2009. Seedling establishment of Asteraceae forbs along altitudinal gradients: a comparison of transplant experiments in the native and introduced ranges. Divers. Distrib. 15: 254–265.

POTGIETER, L. J., D. M. RICHARDSON, AND J. R. U. WILSON. *Casuarina*: biogeography and ecology of an important tree genus in a changing world. Biol. Invasions (in press).

PYŠEK, P., D. M. RICHARDSON, M. REJMÁNEK, G. L. WEBSTER, M. WILLIAMSON, AND J. KIRSCHNER. 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53: 131–43.

R DEVELOPMENT CORE TEAM. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

REJMÁNEK, M., AND D. M. RICHARDSON. 2013. Trees and shrubs as invasive alien species – 2013 update of the global database. Divers. Distrib. 19: 1093-1094.

REJMÁNEK, M. 1989. Invasibility of plant communities. *Biological Invasions. In* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson (Eds.). A Global Perspective, pp. 369–388. John Wiley & Sons, Chichester.

RICHARDSON, D. M., P. PYSEK, M. REJMÁNEK, M. G. BARBOUR, F. D. PANETTA, AND C. J. WEST. 2000. Naturalization and invasion of alien plants-concepts and definitions. Divers. Distrib. 6: 93–107.

ROBERT, R. 1985. Climat et hydrologie à La Réunion étude typologique, étude régionale de l`alimentation et de l`écoulement, Université des Sciences et Techniques du Languedoc, Montpellier, France.

ROCKWOOD, D. L., AND T. F. GEARY. 1991. Growth of 19 exotic and two native tree species on organic soils in southern Florida. Proceedings of the Symposium on Exotic Pest Plants, pp. 283-302. USDI National Park Service Report 1988, Miami.

SASTRE, C., AND J. P. FIARD. 1986. Evolution de la flora terrestre de la Montagne Pelée (Martinique) après les eruptions du XXème siècle. Mise en evidence de bio-indicateurs volcaniques. Compes Rondus Societé Biogeographie 62: 19-42.

SMITH, C. W., AND J. T. TUNISON. 1992. Fire and non-native plants in Hawai'i: Research and management Implications for Native Ecosystems. *In* C. P. Stone, T. J. Tunison, and D. A. Stone (Eds.). Non-native plant Invasions in native ecosystems of Hawai'i: management and research, pp. 394-408. University of Hawai'i Press, Honolulu.

SMITH, C. W. 1998. Pest Plants of Hawai'ian Native Ecosystems. University of Hawai'i, USA: Department of Botany. http://www.botany.Hawai'i.edu/faculty/cw_smith/non-natives.htm. Accessed 27 May 2012.

STRASBERG, D. 1996. Diversity, size composition, and spatial aggregation among trees on 1-hectare rain forest plot at La Réunion. Biodivers. Conserv. 5: 825-840.

STRASBERG, D. 1994. Dynamique des forêts tropicales de l'île de La Réunion: processus d'invasions et de régénération sur les coulées volcaniques. PhD Dissertation, Université de Montpellier II, France.

STRASBERG, D., M. ROUGET, D. M. RICHARDSON, S. BARET, J. DUPONT, AND R. M. COWLING. 2005. An assessment of habitat diversity and transformation on La Réunion Island (Mascarene Islands, Indian Ocean) as a basis for identifying broad-scale conservation priorities. Biodivers. Conserv. 14: 3015–3032.

TCHOUKANSKI, I. 2009. *ET geowizards* (Extension for ArcGIS 9.3). ET SpatialTechniques, Pretoria.

THÉBAUD, C., AND D. STRASBERG. 1997. Plant dispersal in fragmented landscapes: a field study of woody colonization in rainforest remnants of the Mascarene Archipelago, in W. Laurance & R. Bierregaard (Eds). Tropical forest remnants: ecology, conservation, and management. University of Chicago Press, Chicago.

THÉBAUD, C., B. H. WARREN, A. CHEKE, AND D. STRASBERG. 2009. Mascarene islands, biology. *In* R. G. Gillespie, and Clague, D.A. (Eds.). Encyclopedia of Islands, pp. 612-619. California University Press.

TITUS, J. H., AND S. TSUYUZAKI. 2003. Influence of a non-native invasive tree on primary succession at Mt. Koma, Hokkaido, Japan. Plant Ecol. 169: 307-315.

U.S. NATIONAL RESEARCH COUNCIL. 1984. Casuarinas: Nitrogen-fixing trees for adverse sites. National Academy Press, Washington D.C.

VITOUSEK, P. M., AND L. R. WALKER. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. Ecol. Monogr. 59: 247–265.

VITOUSEK, P. M., G. APLET, D. TURNER, AND J. J. LOCKWOOD. 1992. The Mauna Loa environmental matrix: foliar and soil nutrients. Oecologia 89: 372-382.

WALKER, L. R. 1993. Nitrogen fixers and species replacements in primary succession. *In* J. Miles, and D. W. H. Walton (Eds.). Primary Succession on Land, pp. 249-272. Special Publication No. 12 of the British Ecological Society. Blackwell Scientific Publications, Oxford.

WALKER, L. R., R. DEL MORAL. 2003. Primary Succession and Ecosystem Rehabilitation. Cambridge University Press, Cambridge

WEBER, E. 2003. Invasive plants of the World. CABI Publishing, Wallingford.

WHITTAKER, R. H., AND S. A. LEVIN. 1977. The role of mosaic phenomena in natural communities. Theor. Popul. Biol. 12: 117-139.

ZHONG, C., M. GONG, Y. CHEN, AND F. WANG. 1995. Inoculation of *Casuarina* with mycorrhizal fungi and *Frankia*. *In* M. Brundrett, B. Dell, N. Malajczuk, and M. Gong (Eds.). Mycorrhizas for Plantation Forests in Asia, pp. 122-126. ACIAR Proceedings No.62, CSIRO, Canberra.

ZIMMERMAN, N., R. F. HUGHES, S. CORDELL, P. HART, H. K. CHANG, D. PEREZ, R. K. LIKE, AND R. OSTERTAG. 2008. Patterns of primary succession of native and introduced plants in lowland wet forests in Eastern Hawai'i. Biotropica 40: 277–284.

Figures

Figure 4.1. The island of La Réunion in the Mascarene archipelago, eastern Indian Ocean, showing the location of the study site (Grand Brûlé) and the mosaic of lava ages.

Figure 4.2. Spatio-temporal percentage cover of *Casuarina equisetifolia* on Grand Brûlé lava flows for: (A) Cadet (1972), (B) Strasberg & Lepart (1990) and (C) this study (2012). The histogram shows the total area of Grand Brûlé invaded by *C. equisetifolia* in 1972, 1990 and 2012.

Figure 4.3. Combined abundance of *Casuarina equisetifolia* recorded along altitudinal transects of different lava flow ages: (A) Grand Brûlé and (B) the 1986 lava flow outside the caldera.

Figure 4.4. Trends of *Casuarina equisetifolia* over time, derived from synchronic plots (plots where data were available on same lava flow through time) for three surveys: 1972, 1990 and 2012.

Figure 4.5. Conceptual model of (1) natural succession and (2) current successional processes where non-native invasive species now dominate on volcanic substrates of the Piton de la Fournaise Volcano, La Réunion Island (based on GAMs; see Fig. S2, S4). (Photos: L.J. Potgieter). Natural processes succeed in the following order following new lava substrate formation: algae, mosses, lichens, and ferns are the first organisms to colonize; (1A) native wind-dispersed trees such as *Agarista salicifolia* and woody shrubs take advantage of the fissures and colonise over a period of 8 to 15 yrs; (1B) native fleshy-fruited shrubs such as *Antirhea borbonica*, *Aphloia theiformis* and *Sideroxylon borbonicum* proceed to colonise over a period of 15 to 50 yrs; (1C) these shrubs grow to trees over a period of 50 to 200 yrs and form a moderately dense canopy; (1D) growth continues for another 200 yrs to form a mature forest with a dense canopy. Invasive alien species have the potential to co-opt natural processes in several ways: (2A) Alien woody plant species colonise new lava flows within 4 to 8 yrs, four yrs earlier than native species colonisation; (2B) *Casuarina equisetifolia* colonises over a period of 8 to 15 yrs; (2C) as a result of the rapid growth of this species, dense forests can form over a period of 60 yrs. What happens after this stage of succession in which *C. equisetifolia* attains dominance is unknown.

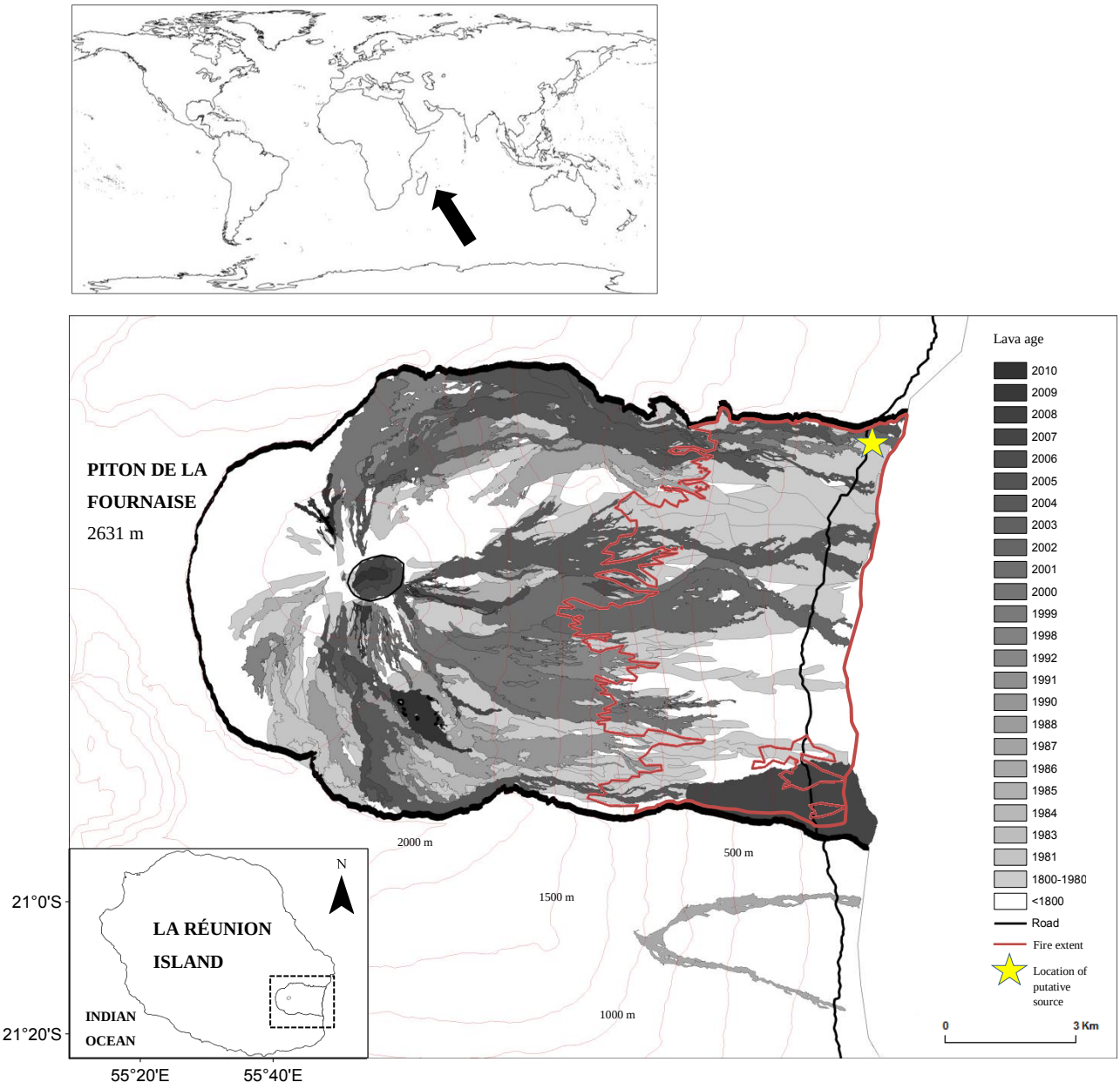
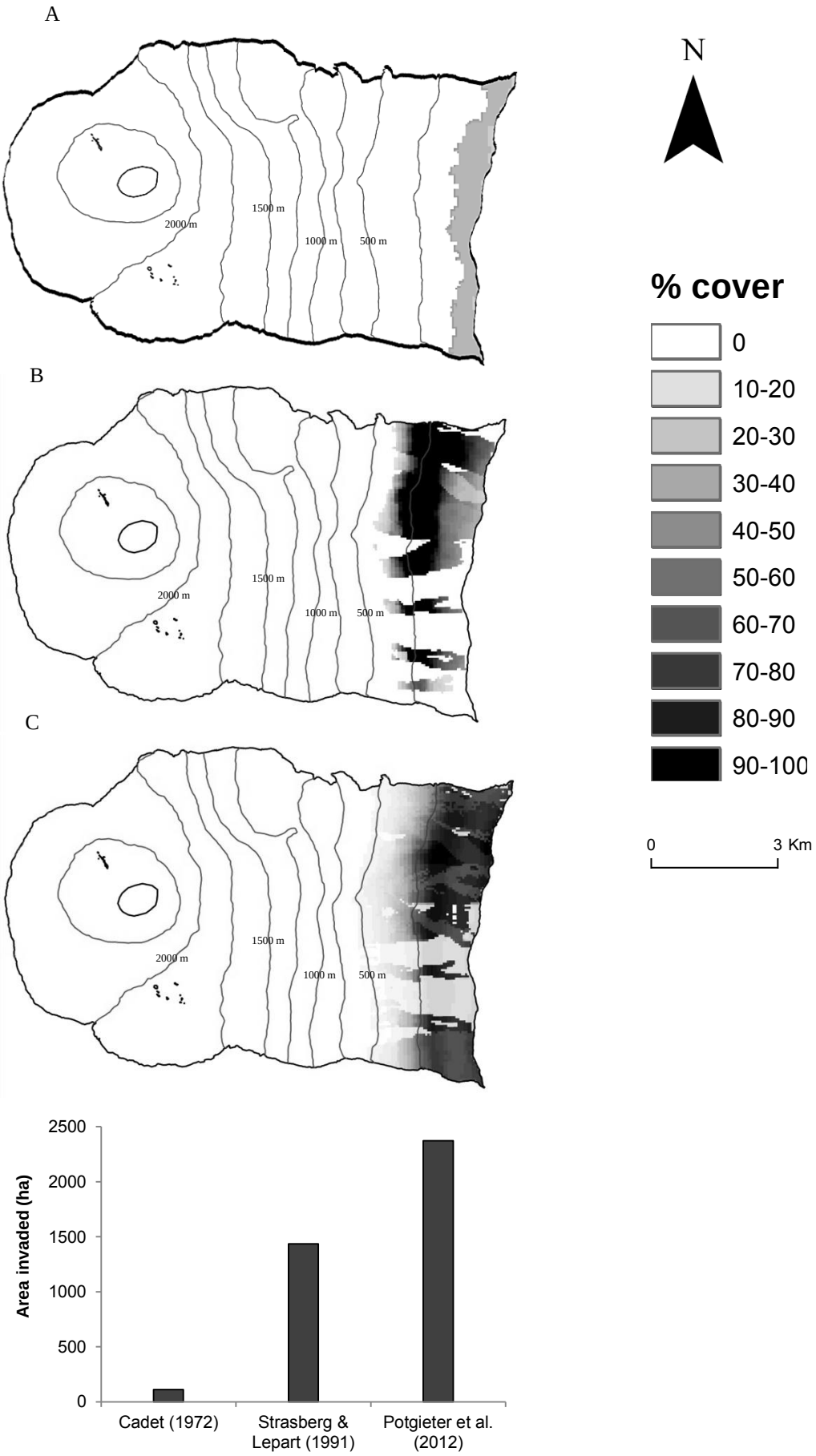


Figure 4.1.



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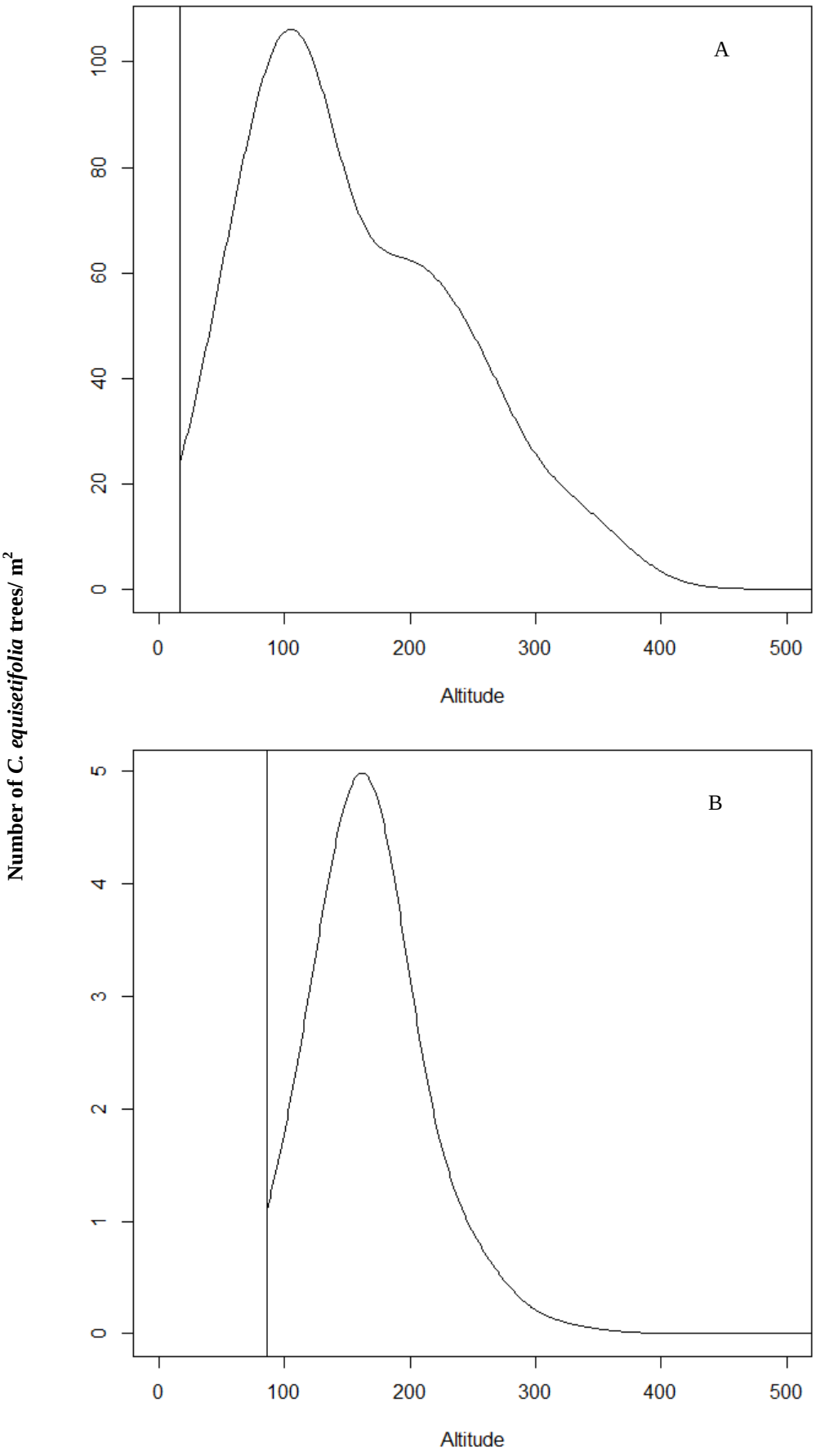


Figure 4.3.

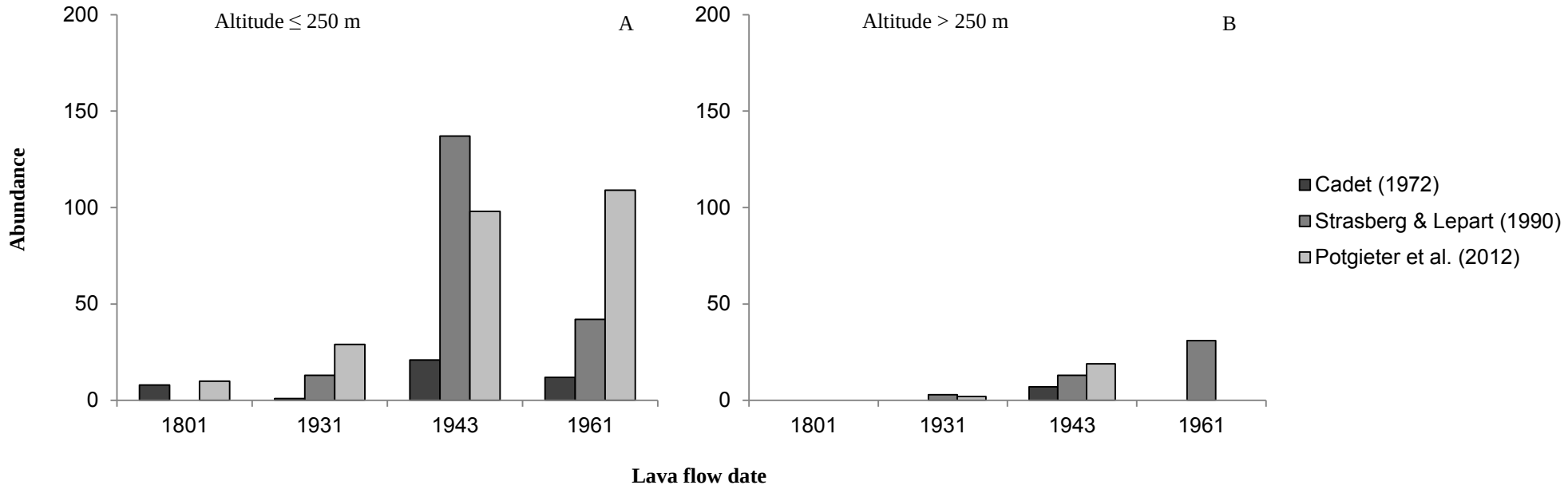

Altitude ≤ 250 m
A
Altitude > 250 m
B
Abundance
200
150
100
50
0
1801
1931
1943
1961
Lava flow date
Cadet (1972)
Strasberg & Lepart (1990)
Potgieter et al. (2012)

Figure 4.4.

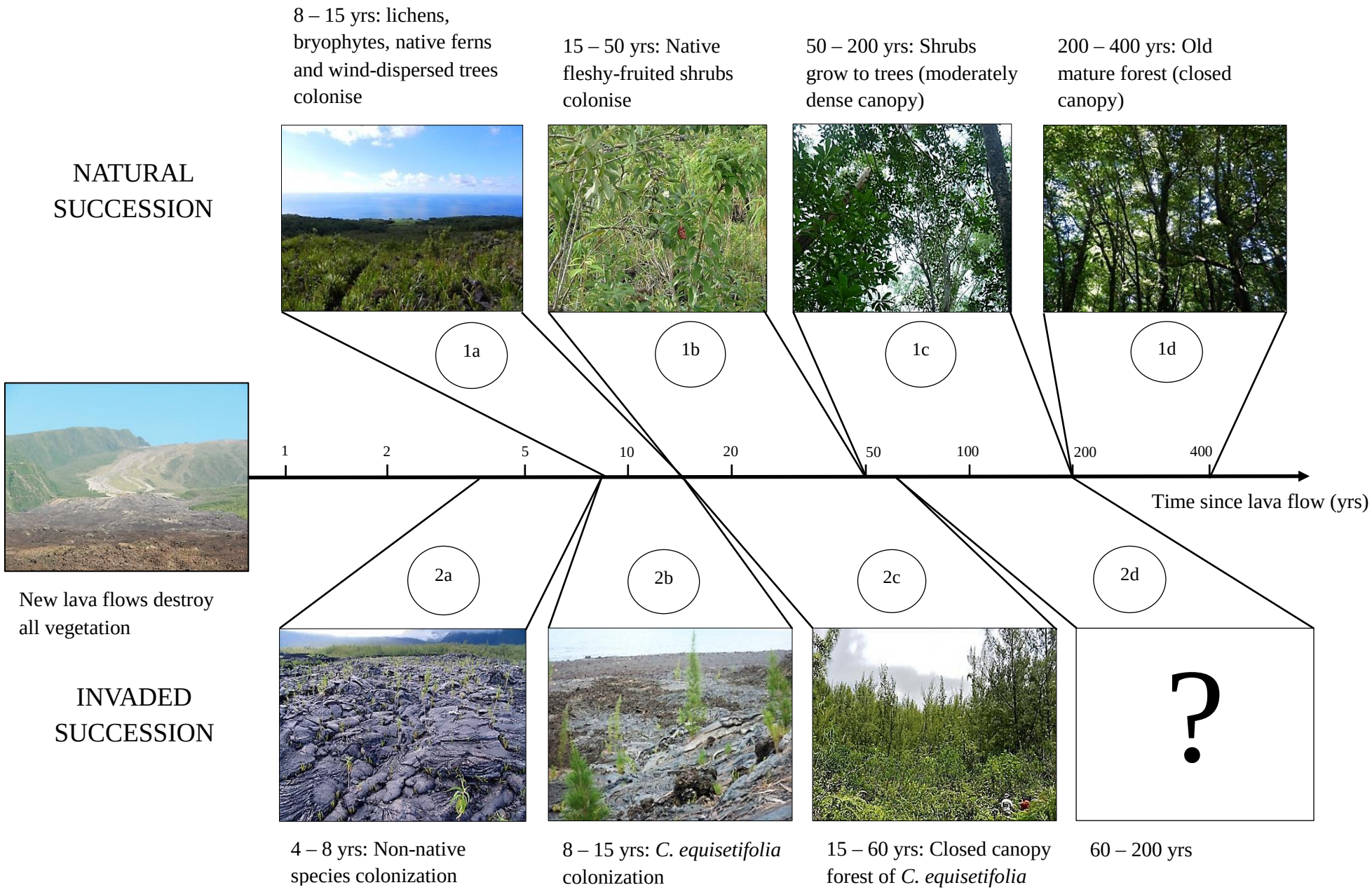

8 – 15 yrs: lichens, bryophytes, native ferns and wind-dispersed trees colonise
15 – 50 yrs: Native fleshy-fruited shrubs colonise
50 – 200 yrs: Shrubs grow to trees (moderately dense canopy)
200 – 400 yrs: Old mature forest (closed canopy)
NATURAL SUCCESSION
1a
1b
1c
1d
1
2
5
10
20
50
100
200
400
Time since lava flow (yrs)
New lava flows destroy all vegetation
2a
2b
2c
2d
?
INVADED SUCCESSION
4 – 8 yrs: Non-native species colonization
8 – 15 yrs: C. equisetifolia colonization
15 – 60 yrs: Closed canopy forest of C. equisetifolia
60 – 200 yrs

Figure 4.5.

Supplementary Tables

Table S4.1. Results of GAM for tree abundance for all three surveys. Null deviance and residual deviance are shown for the overall model, along with marginal reductions in residual deviance (approximate chi-square test) associated with adding each term to the model.

Potgieter *et al*. (2012)					
Null deviance (df): 934.76 (123)					
Residual deviance (df): 545.62 (113)					
Model	AIC	Residual deviance	Reduction in deviance	Explained deviance (%)	p
Altitude	939.61	651.29			
Altitude + lava age	885.52	591.19	60.10	36.75	<0.001
Altitude + lava age + distance to source	847.81	547.48	43.71	41.4	<0.0001
Altitude x distance to source	847.95	545.62	1.856	41.63	>0.05
Strasberg & Lepart (1990)					
Null deviance (df): 1633.33 (113)					
Residual deviance (df): 359.78 (103)					
Model	AIC	Residual deviance	Reduction in deviance	Explained deviance (%)	p
Altitude	692.78	569.76			
Altitude + lava age	627.56	498.54	71.22	69.48	<0.0001
Altitude + lava age + distance to source	493.59	358.56	139.97	78.05	<0.0001

Altitude x distance to source	496.80	359.78	-1.214	77.97	
		Cadet (1972)			
Null deviance (df): 232.07 (83) Residual deviance (df): 185.21 (73)					
Model	AIC	Residual deviance	Reduction in deviance	Explained deviance (%)	p
Altitude	343.62	221.40			
Altitude + lava age	343.51	215.29	6.11	7.23	>0.05
Altitude + lava age + distance to source	323.34	189.12	26.17	18.51	<0.05
Altitude x distance to source	321.43	185.21	3.92	20.19	<0.05

Table S4.2. Results of GAM for tree height for Cadet (1972), and Potgieter *et al*. (2012). Tree heights for Strasberg & Lepart (1990) were not possible to recover. Null deviance and residual deviance are shown for the overall model, along with marginal reductions in residual deviance (approximate chi-square test) associated with adding each term to the model.

Potgieter *et al*. (2012)					
Null deviance (df): 812.80 (197)					
Residual deviance (df): 539.13 (187)					
Model	AIC	Deviance	Reduction in deviance	Explained deviance (%)	p
Altitude	1420.46	702.71	110.09	66.33	<0.0001
Altitude + lava age	1307.12	583.37	119.34	71.77	<0.0001
Altitude + lava age + distance to source	1273.35	543.59	39.78	66.89	<0.0001
Altitude x distance to source	1366.38	640.63	-97.04	78.8	<0.0001
Cadet (1972)					
Null deviance (df): 172.96 (54)					
Residual deviance (df): 132.02 (47)					
Model	AIC	Deviance	Reduction in deviance	Explained deviance (%)	p
Altitude		157.78	40.94	91.22	<0.0001
Altitude + lava age		120.64	37.14	69.75	<0.0001
Altitude + lava age + distance to source		111.40	9.24	64.41	<0.0001
Altitude x distance to source		132.01	-20.61	76.32	<0.0001

Supplementary Figures

Figure S4.1. Plots show the additive effect of each variable on tree abundance and the partial residuals for a) Cadet (1972), b) Strasberg & Lepart (1990), and c) Potgieter *et al*. (2012). Estimates are shown as solid lines, and 95% Bayesian intervals are shown by dashed lines.

Figure S4.2. Plots show the additive effect of each variable on tree height and the partial residuals for a) Cadet (1972), and b) Potgieter *et al*. (2012). Tree heights for Strasberg & Lepart (1990) were not possible to recover. Estimates are shown as solid lines, and 95% Bayesian intervals are shown by dashed lines.

Figure S4.3. Box & Whisker Plot of the number of juvenile trees (< 4 m) on younger lava flows (< 25 yrs old) and that on older lava flows (> 25 yrs old).

Figure S4.4. Detailed conceptual model of (1) natural succession (2) natural and human-mediated disturbances and (3) current successional processes where non-native invasive species now dominate on volcanic substrates of the Piton de la Fournaise Volcano, La Réunion Island.

Additive effects of variable on tree abundance

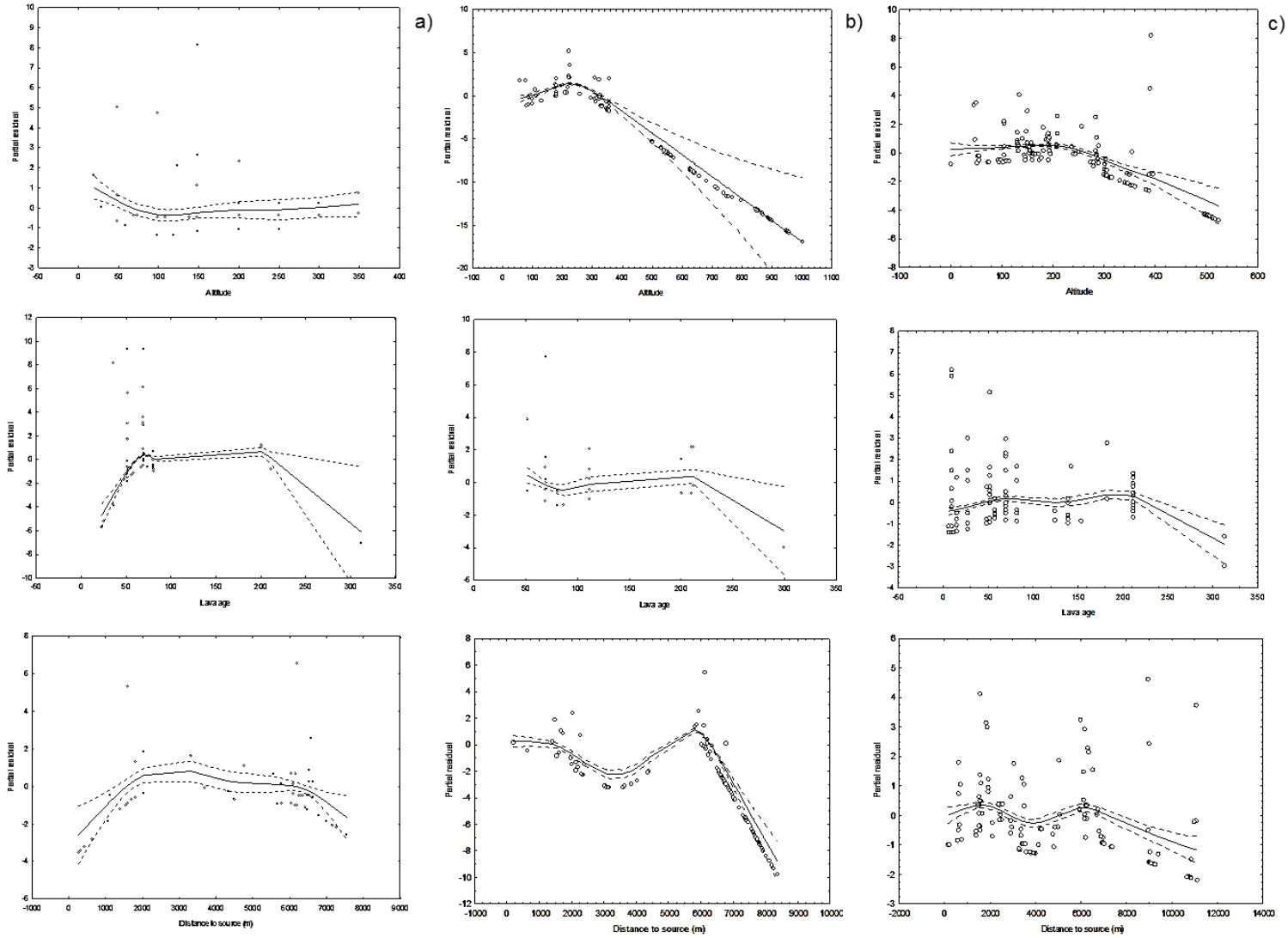
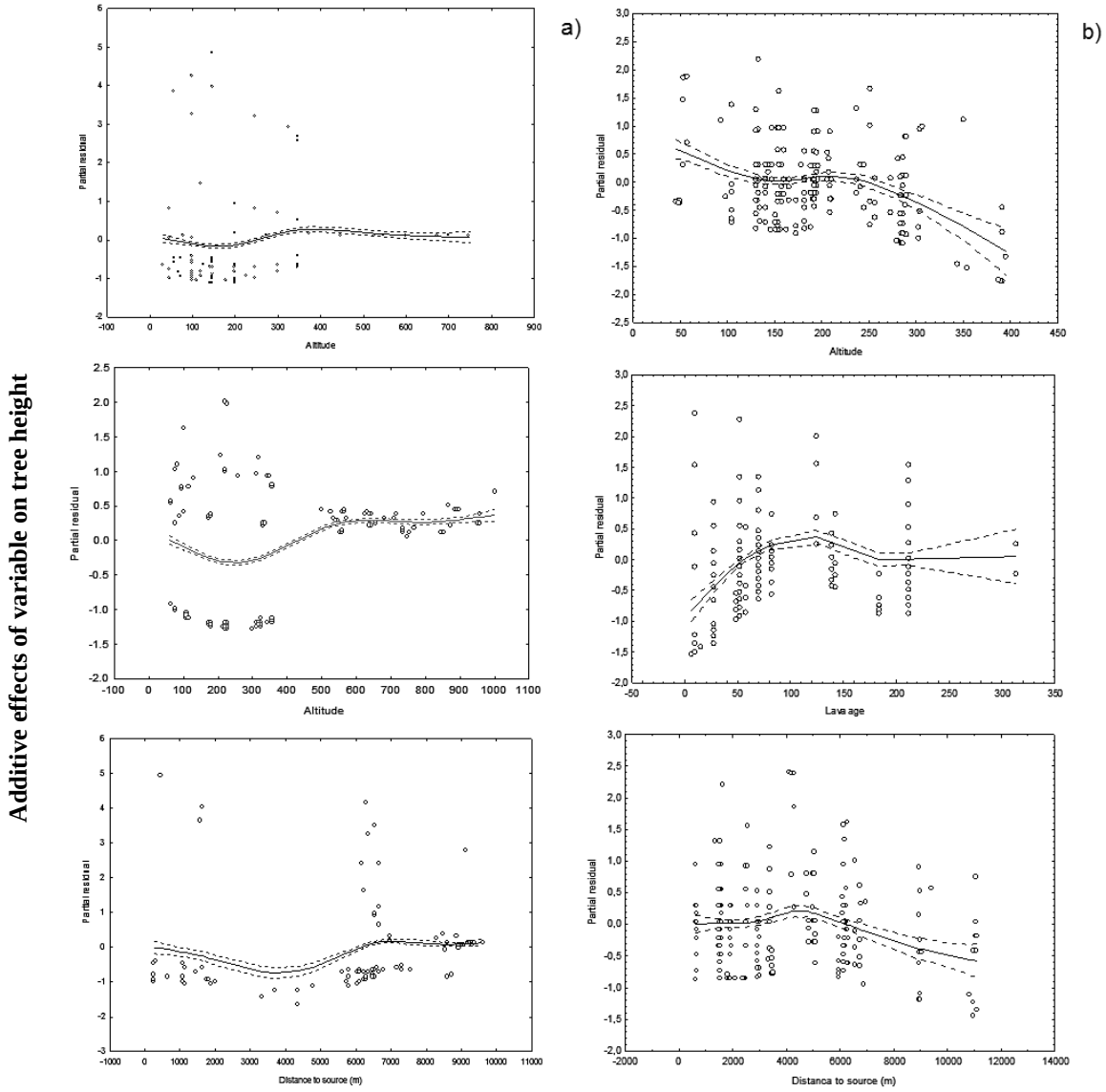


Figure S4.1.



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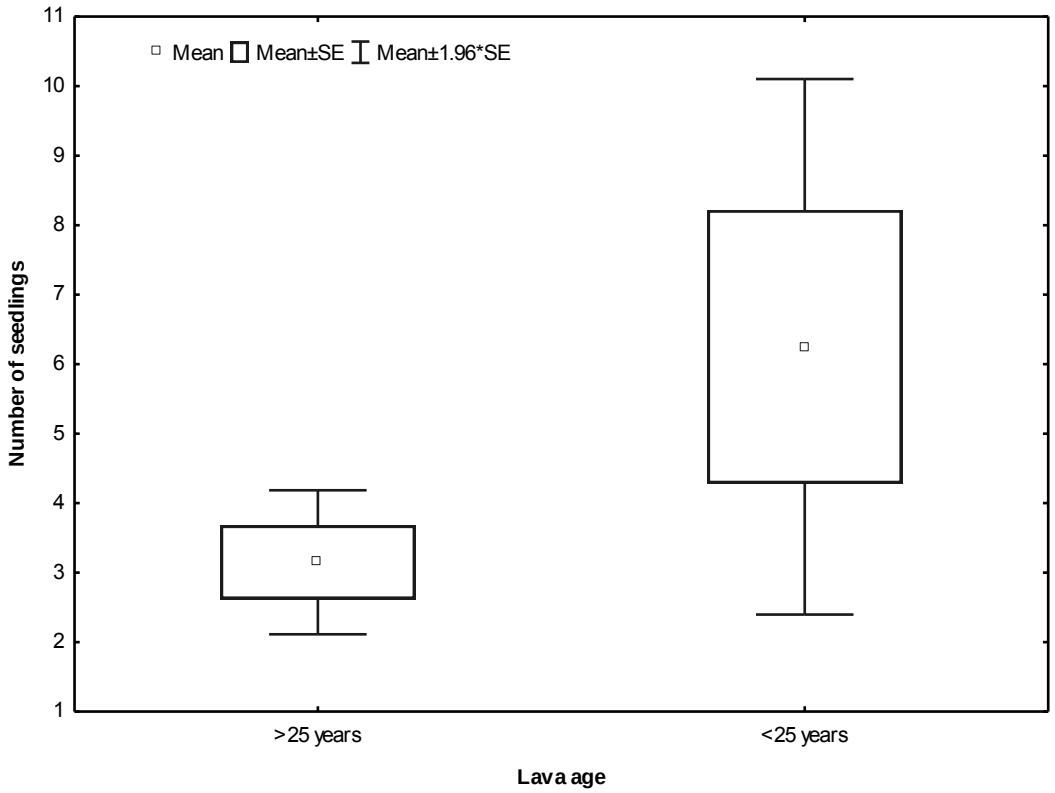

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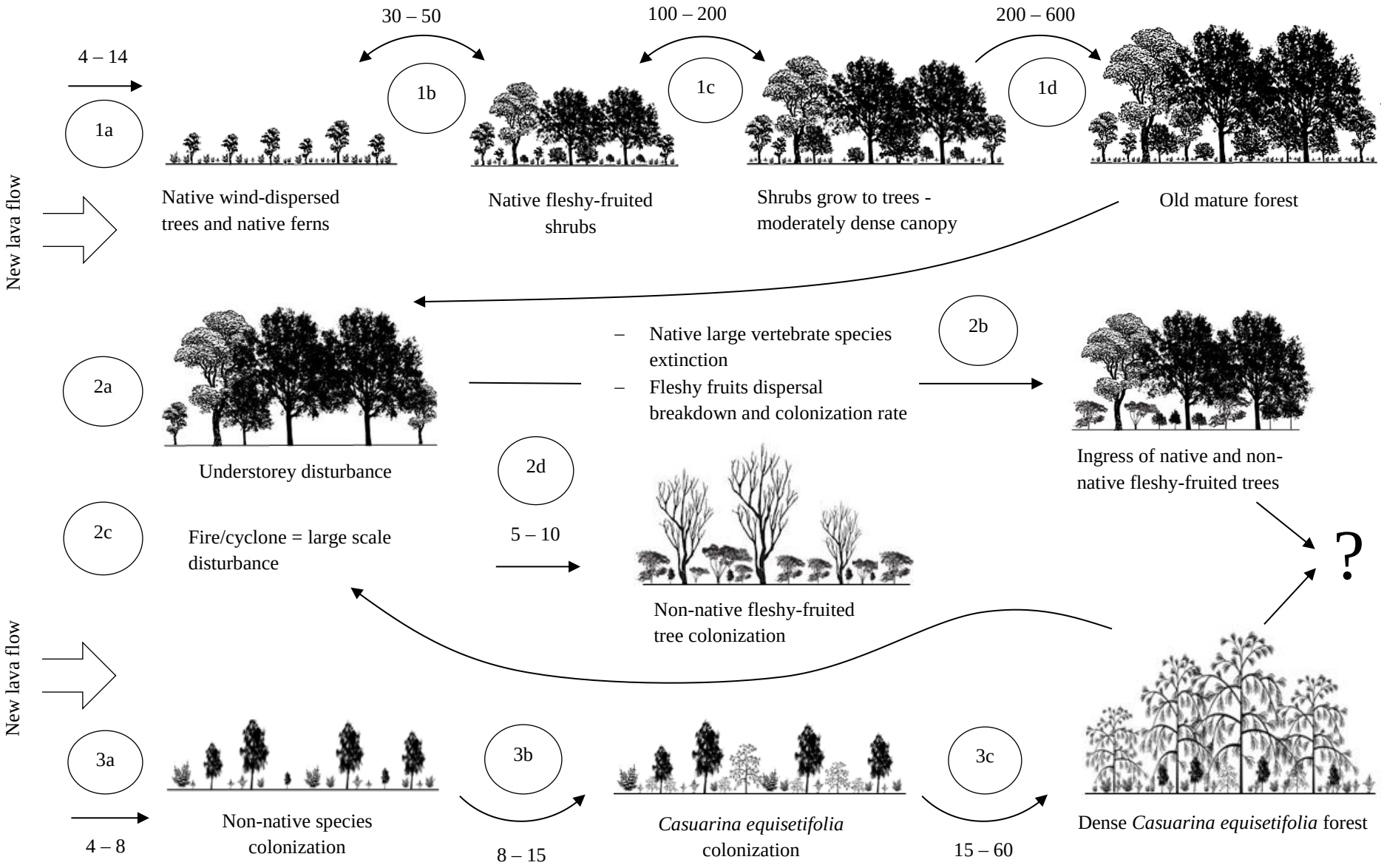
4 – 14
1a
30 – 50
1b
100 – 200
1c
200 – 600
1d
New lava flow
Native wind-dispersed trees and native ferns
Native fleshy-fruited shrubs
Shrubs grow to trees - moderately dense canopy
Old mature forest
2a
Understorey disturbance
– Native large vertebrate species extinction
– Fleshy fruits dispersal breakdown and colonization rate
2b
Ingress of native and non-native fleshy-fruited trees
2c
Fire/cyclone = large scale disturbance
2d
5 – 10
Non-native fleshy-fruited tree colonization
?
New lava flow
3a
4 – 8
Non-native species colonization
3b
8 – 15
Casuarina equisetifolia colonization
3c
15 – 60
Dense Casuarina equisetifolia forest

Figure S4.4.

Chapter 5: Thesis Conclusions

This thesis follows a multi-scale approach and explores the patterns and processes associated with invasiveness of a globally important genus of plants - *Casuarina*. Like other model groups of woody plants (e.g. *Acacia*, *Eucalyptus* and *Pinus*), the global distribution of *Casuarina* has been radically changed by humans in the last few centuries. However, unlike the aforementioned genera, little is known of the global transplant experiment for *Casuarina*, the status of each species in terms of naturalization and invasion, the determinants underlying species' invasion, and the effect *Casuarina* invasions can have on community dynamics. Findings presented in this thesis address these knowledge gaps and assist in developing management approaches that minimise the impacts of invasions while preserving economic, environmental and cultural values of species in their introduced ranges. This chapter presents overall conclusions of the work conducted for the thesis and highlights priorities for further research.

Unlike *Pinus* (Richardson, 2006) and Australian *Acacia* species (Castro-Díez et al., 2011) which are mainly planted around the world for forestry purposes, casuarinas have been widely planted for a variety of reasons, but rarely for direct commercial production. The introduction of many *Casuarina* species to many localities provides useful opportunities to draw important insights on drivers of biological invasions and the effects these invasion have on community structure. Furthermore, this provides an interesting opportunity to compare results from other groups with results from a phylogenetically distinct group.

This thesis underlines the importance of propagule pressure in driving invasion on a global (Chapter 2) and regional scale (Chapter 3), and shows the effect a single invasive species can have on community dynamics at a landscape scale (Chapter 4).

In Chapter 2, I assessed the global introduction history, invasion ecology and the evolution of management approaches of *Casuarina*. Introduced *Casuarina* species with large native ranges are most invasive. Propagule pressure explains much more of the variance in observed invasiveness between *Casuarina* taxa than any known combination of life-history traits. Large-scale plantings of casuarinas in some climatically suitable areas have not yet resulted in large-scale invasions, indicating a substantial global *Casuarina* invasion debt. These results uncover patterns and processes of a novel group of trees in plant invasion ecology, and

emphasize the need to deal with new *Casuarina* invasions that will arise in many parts of the world.

In Chapter 3, I explored which mechanisms determine naturalization of *Casuarina cunninghamiana* and identify areas at risk of invasion in the Western Cape of South Africa. This study confirmed that, on a regional scale, habitat invasibility is primarily determined by propagule pressure of *C. cunninghamiana* in areas where climatic conditions are suitable. This species also naturalizes in regions with suboptimal bioclimatic conditions only in close proximity to planted trees. Climatically suitable areas close to sources of propagules, dams and watercourses are at risk to invasion by *C. cunninghamiana*. I proposed a predictive risk mapping approach for delimiting invasions by species when eradication is not feasible. This should be a useful tool for focussing search efforts in high risk areas, thereby reducing the total cost and effort required for surveillance. *Casuarina cunninghamiana* already occupies a large geographic range in South Africa, in planted stands and increasingly as self-sown stands. Invasion risk is likely to be highest in areas that are climatically most suitable, and that are close to propagule and water sources. The climatic suitability of many areas in the country, the capacity for resprouting and reaching reproductive age early, its rapid growth rate and ability to fix nitrogen make it a high-risk species in South Africa with the potential to transform ecosystems. These results have direct management implications; focussing search efforts in high risk areas, thereby reducing the total cost and effort required for surveillance.

In Chapter 4, I assessed the invasion dynamics of *C. equisetifolia* on the volcanic island of Réunion to explore how the interaction between disturbance and invasion governs successional trajectories. This study found that the extent of invasion by *C. equisetifolia* has increased twenty-fold over the past 40 years. Lava flows have facilitated this spread and *C. equisetifolia* has started to radically change successional trajectories, increasing the rate of succession sevenfold. These findings highlight the need for urgent manage interventions to conserve the small area of remaining native lowland rainforests on Réunion which cover less than 2 % of their original extent.

The results of my thesis have practical implications for invasion biologists, conservation managers, and for assessing the risk of other *Casuarina* species becoming invasive. The findings demonstrate the importance of assessing, in combination, the many facets (i.e. spatial scale, invasion stage, pathways, species traits and characteristics of the recipient environment) that are known to drive biological invasions.

For management to be effective, more research on particular areas and better facilitating mechanisms are required, and conflicts of interest have to be discussed and resolved. Future studies should consider (in combination):

- Identifying species traits as well as characteristics of the recipient habitat that drive invasions.
- Conducting comparative studies of species that are placed at different stages in the introduction-naturalization-invasion continuum.
- Seed-bank dynamics (e.g. seed longevity, seed rain, seed predation and decay, and seed-bank extension).
- Dispersal and recruitment limitations.

A combination of the above-mention recommendations is needed to predict successful invasions. I recommend that future studies adopt a similar approach for other plant groups. Studies of this nature will provide a better understanding of why some introduced species become invasive while others fail and will ultimately assist in managing biological invasions. The work presented in this thesis contributes to understanding the causes and mechanisms of plant invasions and addresses questions of species invasiveness and community invisibility.

References

Castro-Díez, P., Godoy, O., Saldaña, A., Richardson, D.M., 2011. Predicting invasiveness of Australian acacias on the basis of their native climatic affinities, life history traits and human use. Diversity and Distributions 17, 934–945.

Richardson, D.M., 2006. *Pinus*: a model group for unlocking the secrets of alien plant invasions? Preslia 78, 375–388.